

A taxonomic revision of the ant subgenus *Coptoformica* Mueller, 1923 (Hymenoptera, Formicidae)

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Seifert B. 2000. — A taxonomic revision of the ant subgenus *Coptoformica* Mueller, 1923 (Hymenoptera, Formicidae). *Zoosystema* 22 (3) : 517-568.

ABSTRACT

A total of 3800 specimens of the ant subgenus *Coptoformica* from the whole Palaearctic was studied, 2800 specimens of which were evaluated morphometrically giving 22000 primary data. Comments on allometries and on the taxonomic significance of characters are given. Keys and comparative tables of morphometric characters include workers, females, and males. Out of 28 taxa described from this region up to the present, 15 taxa are synonymised while 11 taxa are demonstrated as good species by high-precision stereomicroscopy, chorology, and comparative biology. Two taxa remain as *incertae sedis*. Taxonomic changes to systems previously used include the demonstration of the different species identity of *Formica foreli* Emery, 1909 and *F. pressilabris* Nylander, 1846, the synonymisation of *F. goesswaldi* Kutter, 1967, *F. naefi* Kutter, 1957, and *F. tamarae* Dlussky, 1964 with *F. foreli*, the synonymisation of *F. brunneonitida* Dlussky, 1964 and of *F. fossilabris* Dlussky, 1964 with *F. forsslundi* Lohmander, 1949, the synonymisation of *F. dluskyi* Bolton, 1995 with *F. manchu* Wheeler, 1929, the synonymisation of *F. nemorialis* Dlussky, 1964 with *F. exsecta* Nylander, 1846, and the description of *F. fennica* n. sp. from South of the Finland and the Caucasus. Proximities to the Asian species *F. manchu* Wheeler, 1929 point to a Siberian origin of *F. fennica*. The synonymisation of the taxon *etrusca* Emery, 1909 with *exsecta* and the treating of the taxon *mesasiatica* Dlussky, 1964 as endemic Middle Asian species separate from *exsecta* are doubtful decisions that should be checked by future revisors with more extensive and more adequate approaches.

KEY WORDS

Formicidae,
subgenus *Coptoformica*,
taxonomic revision,
Palaearctic.

RÉSUMÉ

Révision taxonomique des fourmis du sous-genre *Coptoformica* Mueller, 1923 (Hymenoptera, Formicidae).

Parmi 3800 spécimens étudiés de fourmis du sous-genre *Coptoformica* de la région palaéarctique, 2800 ont été étudiés par des méthodes morphométriques, produisant ainsi 22000 données primaires. Des commentaires sur les allométries et la signification taxonomique des caractères sont proposés. Les clés et les tables morphométriques des caractères concernent les ouvrières, les femelles et les mâles. Parmi les 28 taxa décrits jusqu'à présent dans cette région, 15 taxa sont synonymisés et il est démontré par des données de stéréomicroscopie de haute précision, de chorologie et de biologie comparative que 11 taxa sont des espèces valides. Deux taxa restent *incertae sedis*. Les changements taxonomiques par rapport aux systèmes utilisés précédemment incluent la démonstration de la différence spécifique de *Formica foreli* Emery, 1909 et *F. pressilabris* Nylander, 1846, la mise en synonymie de *F. goesswaldi* Kutter, 1967, *F. naefi* Kutter, 1957 et *F. tamarae* Dlussky, 1964 avec *F. foreli*, la mise en synonymie de *F. brunneonitida* Dlussky, 1964 et de *F. fossilabris* Dlussky, 1964 avec *F. forsslundi* Lohmander, 1949, la mise en synonymie de *F. dluskyi* Bolton, 1995 avec *F. manchu* Wheeler, 1929, la mise en synonymie de *F. nemoralis* Dlussky, 1964 avec *F. exsecta* Nylander, 1846 et la description de *Formica fennica* n. sp. du Sud de la Finlande et du Caucase. La proximité de l'espèce d'Asie *F. manchu* Wheeler, 1929 indique une origine sibérienne pour *F. fennica*. La mise en synonymie du taxon *etrusca* Emery, 1909 avec *exsecta* et le traitement du taxon *mesasiatica* Dlussky, 1964 comme une espèce endémique de l'Asie centrale, séparée de *exsecta*, sont des décisions incertaines qui devront être vérifiées par des réviseurs ultérieurs disposant d'approches plus générales et plus adéquates.

MOTS CLÉS

Formicidae,
sous-genre *Coptoformica*,
révision taxonomique,
Palaéarctique.

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Taxa with insufficient descriptions and unavailability of types *incertae sedis*

Key and comparative tables to workers

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INTRODUCTION

Twenty eight taxa belonging to the subgenus *Coptoformica* Mueller, 1923 have been described

up to the present: 18 from Europe and 10 from Asia. A taxonomic revision of the group, which should include investigation of type specimens, numeric evaluation of populations, and attempts to verify the proposed status of the considered taxa, has not been published so far. A most helpful contribution to the taxonomy of *Coptoformica* was given by Agosti (1989) in his thesis. However, all taxonomic acts performed in this paper have no validity according to the *International Code of Zoological Nomenclature*. Furthermore, the precision of data recording, and the number of measured specimens, was not adequate to demonstrate delicate interspecific differences. The consequence was a certain lumping bias. For example, Agosti recognised five good species for Europe, but evidence is presented in this paper that there are at least seven good species with differing biology. Nevertheless, the thesis of Donat Agosti is a most valuable synopsis of the whole subgenus and has provided helpful ideas on the taxonomic significance of certain morphological characters.

The material available from Asia was poor; only 60 different samples with 250 specimens were examined, and the failing response of the curators in St Petersburg prevented access to further material from this huge territory. In contrast, 500 samples with 3 500 specimens were examined from Europe. As a consequence, a profound revisionary work on a broad basis of evidence was only possible for the W Palaearctic range. Nevertheless, types or paratypes of all Asiatic taxa, except for *fossilabris*, were available and useful information on the type material that was not available from Moscow and St Petersburg is found in the thesis of Donat Agosti. The maintenance of *Formica bruni* Kutter, 1967 and the introduction of *Formica fennica* n. sp. in this paper have thus a reasonable basis.

ABBREVIATIONS

The institutions or important private collections from which material was studied have the following acronyms:

NHM Basel	Naturhistorisches Museum, Basel, Switzerland;
ZMHU	Zoologisches Museum der

IRSN	Humboldt Universität Berlin, Germany;
coll. Douwes	Institut royal des Sciences naturelles de Belgique, Bruxelles; collection of Per Douwes, Lund, Sweden;
DEI	Deutsches Entomologisches Institut Eberswalde, Germany;
MHN	Muséum d'Histoire naturelle Genève, Switzerland;
MCSN	Museo Civico di Storia Naturale Genova, Italy;
SMN	Staatliches Museum für Naturkunde, Goerlitz, Germany;
MCZ	Museum of Comparative Zoology of the Harvard University, Cambridge, Massachusetts, USA;
FMNH	Finnish Museum of Natural History, University of Helsinki, Finland;
MZ	Musée de Zoologie, Lausanne, Switzerland;
RNH	Rijksmuseum van Natuurlijke Historie Leiden, Netherlands;
MNHN	Muséum national d'Histoire naturelle, Paris, France;
ZMLSU	Zoological Museum of the Lomonosov State University Moskva, URSS;
coll. Schulz	collection of Andreas Schulz, Leichlingen, Germany;
NHRM	Naturhistoriska Riksmuseet Stockholm, Sweden;
ZM	Zoological Museum of the University of Turku, Finland;
ZIPAS	Museum of the Zoological Institute of the Polish Academy of Sciences, Warszawa, Poland;
coll. Werner	collection of Petr Werner, Praha, Czech Republic;
NHM Wien	Naturhistorisches Museum, Wien Austria.

MATERIAL STUDIED

A total of 560 different samples with 3750 specimens of *Coptoformica* was studied. 89% of this material are originated from Europe and 11% from Asia. 1367 workers, 281 queens, and 109 males from 470 different series were evaluated numerically for 13, 13, and 8 characters respectively, giving 22000 primary data on morphology.

METHODS AND TERMINOLOGY

All measurements were made on mounted and dried specimens using a goniometer-type pin-holding device, permitting endless rotations around X, Y, and Z axes. A Wild M10 stereomicroscope equipped with a $1.6\times$ planapochromatic objective was used at magnifications of $50\text{--}320\times$. The maximum possible magnification to keep a structure within the range of the ocular micrometer was used. A mean measuring error of $\pm 0.4\text{ }\mu\text{m}$ is given for small and well-defined structures, such as hair length, but may reach $4\text{ }\mu\text{m}$ for measures $> 1700\text{ }\mu\text{m}$ with difficult positioning and high influence of air humidity. To avoid rounding errors, all measurements were recorded in μm even for characters for which a precision of $\pm 1\text{ }\mu\text{m}$ is impossible. In order to reduce irritating reflections of the cuticular surfaces and to get an improved visualization of the microsculpture, a plastic diffuser was positioned as close as possible to the specimen. The SEM pictures were made on dehydrated and gold-coated specimens with a ZEISS DSM 940 at magnifications of $125\text{--}2000\times$.

Setae, also called pilosity or simply "hairs", are differentiated from pubescence hairs in having a much larger diameter, usually $4\text{--}8\text{ }\mu\text{m}$ in setae and $1\text{--}2\text{ }\mu\text{m}$ in pubescence (Fig. 8). All seta counts (nMET, nCOXA, nHTFL, TERG, ClySet, OceSet) are restricted to standing setae projecting $> 10\text{ }\mu\text{m}$ from cuticular surface.

CL. Maximum cephalic length in median line; the head must be carefully tilted to the position with the true maximum. Excavations of occiput and/or clypeus reduce CL. Thus, in *Coptoformica*, CL is much smaller than the commonly used "overall head length in full face view" that includes the occipital corners and cannot be measured precisely without special devices.

ClyPub. Unilateral number of pubescence hairs surpassing the frontolateral clypeal margin by more than $10\text{ }\mu\text{m}$; counting begins at the sagittal level of the tentorial pit (a small but deep impression at the caudolateral clypeal margin, marked with an arrow in Fig. 3) and ends at the lateralmost portion of the clypeus; the number of both sides is halved.

ClySet. The presence of different setae positions on clypeus (Fig. 1C). The values 1 to 5 mean different distributional levels:

1. Only apical setae based in the frontal clypeal margin and directed frontad are present or whole clypeus completely without setae;
2. Single postapical clypeal setae present; these second level setae are based a short distance caudal from the anterior clypeal margin and are normally suberect;
3. Single standing setae are found at central portions of clypeus;
4. Standing setae are found at posterior portions of clypeus;
5. Whole surface of clypeus with standing setae.

CS. Cephalic size; the arithmetic mean of CL and CW, used as a less variable indicator of body size.

CW. Maximum cephalic width; this is either across, behind, or before the eyes.

EyeHL. The length of the longest hair on the eyes including minute hairs visible at magnifications $\geq 150\times$ (Fig. 9).

GLANZ. This is a subjective estimation of the brilliance of the dorsal head surface in queens at magnifications of $80\times$. The minimum GLANZ value of 1.0 means the whole surface of head is matt and microsculptured. The maximum GLANZ value of 3.0 means the whole dorsal head is brilliantly shining; widely spaced and very weak microsculpture lines may occur. Values between 1.0 and 3.0 indicate different degrees of intermediates.

ML. Mesosoma length in the alates; measured in lateral view from the caudalmost portion of propodeum to the frontalmost point of the anterior pronotal slope (i.e. not to the frontalmost point of the whole mesosoma that is frequently concealed by the occiput!).

MnHL. The length of the longest standing seta on mesonotum. If the differentiation between setae and pubescence is difficult, larger pubescence hairs may be considered.

nCOXA. Setae number on the frontal face of forecoxae. The number on both forecoxae is halved.

nHTFL. Setae number on the outer edge of the hind tibial flexor side, i.e. the edge positioned laterally when the hind tibia is directed caudad.

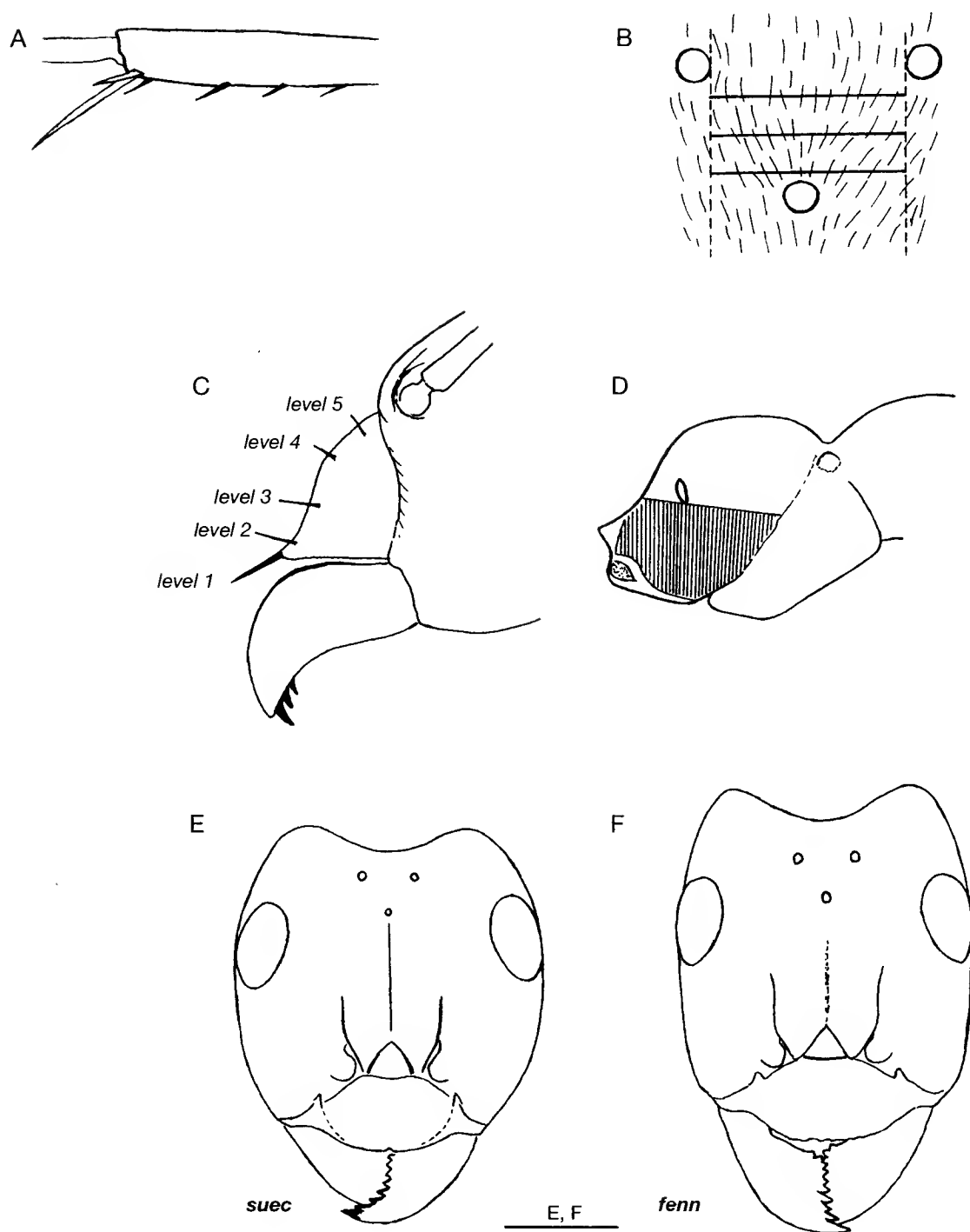


FIG. 1. — **A**, count of nHTFL. The seta count excludes the apical seta on outer flexor apex representing a counterpart to the big spur on the inner flexor apex (spur and apical seta left empty) and includes all remaining setae on outer margin of hind tibia flexor profile (filled blackish); **B**, position of measuring lines in the ocellar triangle for calculation of the character sqrtPDF; **C**, anterior head in profile; position of the different levels of clypeal setae to describe the character ClySet; **D**, caudal mesosoma; the seta count nMET is restricted to the hatched area; **E**, *Formica suecica* worker, short head type with rounded outlines; **F**, *Formica fennica* worker, long head type with more linear outlines. Scale bar: 500 μ m.

Not included in the count is the always existing strong hair on outer flexor apex representing a counterpart to the big spur on the inner flexor apex (spur and apical seta left empty in Fig. 1A). If there is rich pilosity with different size classes of setae (e.g., in *exsecta*), only the first order setae are counted. The number of both tibiae is halved.

nMET. Unilateral number of standing setae on lateral metapleuron and ventrolateral propodeum (hatched area in Fig. 1D), i.e. the area below the level of propodeal spiracle but excluding those hairs fringing the metathoracic gland and those standing on the ventrolateral edge of metapleuron. The number of both sides is halved.

nPN. Number of standing setae on pronotum.

OccHD. The hair projection at occipital corners; the distance of the most projecting hair tips (setae or pubescence) from cuticular surface of occipital head in dorsal view.

OceSet. Presence (score "1") or absence (score "0") of standing setae in the lateral region of the ocellar triangle (Fig. 11).

SL. Maximum straight line scape length excluding the articular condyle.

sqrtPDF. Square root of pubescence distance in the area between the posterior (lateral) and the frontal (mid) ocellus. The number of pubescence hairs n crossing a transverse measuring line of length L is counted, hairs just touching the line are counted as 0.5. The pubescence distance PDF is then given by L/n . The length of the measuring lines is defined by the distance of the inner margins of posterior ocellae. Three transverse lines of this length are set: the first line a short distance frontal to the hind ocellae, the second between the hind and the frontal ocellus, and the third a short distance caudal of the frontal ocellus. The three counts are averaged (Fig. 1B). In order to normalise the positively skewed distributions, the square root of PDF is calculated. Exact counting is promoted by clean surfaces and flat, reflexion-reduced illumination. The counting was performed at magnifications of 320 \times . Surface spots with torn-off pubescence were excluded from measuring.

sqrtPDG. Square root of pubescence distance on the dorsomedian part of first gaster tergite. Principles of counting as in sqrtPDF. In case of

surface damage or deformation, the second tergite may be used. To reduce accidental errors, six countings along six differently positioned, transverse measuring lines of 400 μ m length are averaged. In order to normalise the positively skewed distributions, the square root of PDG is calculated.

TERG. The frontalmost gaster tergite with at least one standing seta. In species with reduced pilosity, the posterior tergite margins must be scrutinised carefully in search of a hair fitting the definition of seta.

The method for calculating discriminant scores for workers and queens of *Formica pressilabris* and *foreli* was as follows.

If necessary, the data of a character X_i to X_n were square-root-transformed to approximate normal distributions. A discriminant $d(x_i)$ was then calculated as

$$d(x_i) = LG \frac{f_A(x_i)}{f_B(x_i)} \quad (1)$$

where $f_A(x_i)$ and $f_B(x_i)$ are the function values of the normal distributions of species A and B for the character X_i . A discriminant score D is then calculated for n characters as

$$D = \frac{1}{n} \sum_{i=1}^n LG \frac{f_A(x_i)}{f_B(x_i)} \quad (2)$$

This discriminant score does not consider correlations between the characters and could overestimate single causes, e.g., pleiotropic effects of single genes. This overrating can be equalised if a discriminant vector $D(x)$ is calculated for any possible character combination $X_i X_j$ with

$$D(x) = \frac{(n-2)!}{n!} \sum_{i=1}^{n-1} \sum_{j=i+1}^n (d(x_i) W(x_i) + d(x_j) W(x_j)) (1 - r_{ij}) \quad (3)$$

where r_{ij} is the absolute value of the arithmetic mean of the linear correlation coefficients of species A and B for characters X_i and X_j (calculation of arithmetic mean with consideration of the signs). $W(X_i)$ and $W(X_j)$ are weightings compensating for the overall validity losses caused by the factor $(1 - r_{ij})$, with $W(X_i)$ meaning

$$W(X_i) = \sum_{\substack{j=1 \\ j \neq i}}^n r_{ij} \quad (4)$$

If not otherwise stated, statistic tests testing the equality of mean values are: a *t* test when an *F* test proved the equality of the variances; otherwise a modified *t* test with corrected degrees of freedom according to Welch (1947) was applied.

COMMENTS ON ALLOMETRIES

Allometries are negligible in *Coptoformica* in most of the metric characters used in this paper. This refers in particular to the relations between CL/CW, SL/CL, and SL/CW which are practically isometric in *Coptoformica* but show clear negative allometries in other related groups as the subgenera *Serviformica*, *Formica* s. str., and *Raptiformica* (Table 1) or in the tribes Lasiini and Camponotini (Seifert 1989, 1992, 1996, 1997). The insignificant dependency of these indices from body size in *Coptoformica* allows their direct use in species discrimination without the need for allometric corrections. No significant allometries are detectable within the subgenus *Coptoformica* in further characters such as EyeHL, TERG, nCOXA, sqrtPDF, and sqrtPDG. A consideration of allometries may be indicated in the characters nHTFL, and nMET. nHTFL grows with 100 μ m CL increase by 18.0% (as arithmetic mean of eight considered species) and nMET by 22.0% (as arithmetic mean of the two species with nMET > 0).

COMMENTS ON THE TAXONOMIC SIGNIFICANCE OF CHARACTERS

Tables 6 to 10 indicate the discriminative power of the 17 characters defined above. Head indices such as SL/CL and CL/CW in workers and queens or absolute measures such as ML in queens may have considerable taxonomic importance but the main contribution is undoubtedly given by setae and pubescence characters. Different authors have expressed controversial opinions on the value of pubescence characters (Dlussky 1967; Dlussky & Pisarski 1971; Collingwood 1979; Agosti 1989) and the pro-

TABLE 1. — Allometries of head indices in three subgenera of *Formica*. Given is the change of an index in percent of the species-specific means for an CL increase of 100 μ m. The ratios in *Coptoformica* can be considered as isometric.

	Subgenus <i>Coptoformica</i> (1020 workers of 8 species)	Subgenus <i>Serviformica</i> (1025 workers of 10 species)	Subgenus <i>Formica</i> s. str. (1545 workers of 6 species)
CL/CW	+ 0.206%	- 0.897%	- 0.903%
SL/CL	- 0.057%	- 0.720%	- 0.397%
SL/CW	+ 0.142%	- 1.616%	- 1.294%

blem needs therefore a more detailed consideration. Agosti (1989) regarded tergite pubescence density as insignificant for species discrimination in *Coptoformica* except for the extreme situation in *Formica fukaii*. My own results give only partial confirmation of Agosti's view. The sqrtPDG and sqrtPDF data (Tables 6-9) indicate that pubescence on gaster tergites may be useful in several cases and demonstrate convincingly the outstanding importance of pubescence distance in the ocellar triangle. As a general intraspecific rule in *Coptoformica*, the number of pubescence hairs per unit square of body surface shows a strong negative correlation with the mean length of pubescence hairs whereas pubescence distance, as defined here, shows a weakly positive correlation. This is important in the context of frequently used key termini such as "distance between pubescence hairs smaller than their length". In a sample of 194 *Formica exsecta* workers and referring to median centre of second gaster tergite, the square root number of pubescence hairs per 1 mm² (sqrtGPD) and that of pubescence distance (sqrtPDG) can be described as function of mean pubescence hair length (GPL):

– sqrtGPD = - 0.8030 GPL + 56.6 (*r* = - 0.799, *n* = 194) and

– sqrtPDG = + 0.1564 GPL + 0.545 (*r* = + 0.635, *n* = 194).

In the given set of data, mean and standard deviation are 472 \pm 253 in GPD, 57.5 \pm 18.7 in PDG, 21.08 \pm 5.23 in sqrtGPD, 7.46 \pm 1.28 in sqrtPDG, and 44.26 \pm 5.20 in GPL. The coefficients of variation are 53.6% in GPD, 32.5% in

PDG, 24.8% in sqrtGPD, but only 17.1% in sqrtPDG. As a consequence, measures as sqrtPDG and sqrtPDF have an improved discriminative power compared to pubescence density numbers.

Some characters traditionally considered in *Coptoformica* were abandoned and are shortly commented here (for situation in males see section 11).

Clypeal depression. The intraspecific variation of the depth and shape of this structure is too large to have diagnostic value.

Maxillary and labial palps. These structures are almost useless for species discrimination. The basic palp formula in the species considered here is 6,4. Due to fusion of terminal maxillary palp segments this formula may vary intranidally (e.g., 6,4-5,4 in *bruni*, *forsslundi*, and *pisarskii* or 6,4-4,4 in *foreli*; intranidal variation in other species not investigated, see also Agosti 1989). Similarly, the maxillary palp length index (PAI = length of maxillary palps/CW) shows high intranidal variation and has a low discriminative value. There are statistical differences of PAI between some species but exactly these species are much better separated by other characters.

Mesosomal shape. In workers, intraspecific variation of mesosomal shape is much larger than interspecific differences (see also Agosti 1989). In queens, Kutter (1977) has used a "thoracic index" (ML/mesosoma width before the tegulae) for the separation of his taxa *naefi* and *goesswaldi* from *foreli* and *pressilabris*. This index is without taxonomic value. My own investigations in several *Lasius* and *Formica* queens have shown mesosomal width to have definitely higher coefficients of variation than mesosomal length and other body measures. This could be the result of different larval nutrition or of a selection for a functional polymorphism, i.e. wide-breasted queens with strong wing muscles might perform a long-range flight while the narrow-breasted queens stay in the vicinity of their mother colonies. In *Coptoformica*, this queen polymorphism might be a functional analogy to the well-known male size polymorphism. Wide- and narrow-breasted queens are known in *foreli*, *bruni*, and *forsslundi*.

Metasternal process. This structure is almost identical in all species considered.

Petiole shape. There may be statistical differences in depth and shape of the dorsal excavation between some species but the enormous intraspecific variation invalidates this character.

Colour. The very similar average colour pattern throughout the group and its dependency upon climatic and nutritive factors and genetic polymorphism excludes the use of colour in species identification. Similar to other *Formica* species (see Lange 1956; Dlussky 1967; Pisarski 1981; Seifert 1997), the ratio of red pigmentation *vs* blackish pigmentation increases with growing body size (i.e. better larval nutrition) and with growing xerothermy of the nest spot.

DIAGNOSIS OF THE SUBGENUS *COPTOFORMICA* MUELLER, 1923

The Palaearctic subgenus *Coptoformica* Mueller, 1923 belongs to the ant genus *Formica* and is most probably monophyletic. All *Coptoformica* species constantly share the following character combination:

- a) occipital margin of head both in big and small specimens deeply excavated; depth of excavation 4.9-9.6% of overall head width (CW);
- b) mandibles always with one to three prebasal denticles, i.e. denticles positioned caudolateral of the true masticatory border;
- c) dorsal crest of the petiolar scale always excavated; depth of excavation usually 3-10% of maximum scale width. Petiole scale thin in lateral view;
- d) isometry of index SL/CW (see section 4).

This character combination is not found in any other species of the tribe Formicini. The genus *Rossomyrmex* shows character (a) but has a very thick, petiole scale and no prebasal mandibular denticles. Members of the Nearctic *Formica exsectoides* group occasionally show prebasal denticles, but have a weakly or not excavated occiput (0-3.5% of CW), differ in petiolar shape, and show a negative allometry of SL against CW. The monophyly of *Coptoformica* was also suggested by

Agosti (1989). An elevation to genus rank seems acceptable but is not performed here in the absence of a profound phylogenetic study of all species groups presently combined in the genus *Formica* Linnaeus, 1758.

A unique biological trait not found in other members of the tribes Formicini and Lasiini is shared by obviously all *Coptoformica* species; it is the mode of constructing the hull of the vegetable nest dome with finely cut pieces of herbs (preferentially grasses). This peculiar behaviour is also observed in *Formica suecica*, although this species rarely uses this technology. The effective cutting of grasses and the painful biting of *Coptoformica* ants that is known to every investigator can be explained by an altered mechanical system of mandible and adductor muscle which is considered as autapomorphy (Dietrich 1998). Dietrich compared mechanical parameters of the mandible adductor system in *Coptoformica exsecta* and *Formica pratensis*. An elongated lever between the mandibular condyles and the attachment point of adductor muscle in combination with a shortened lever between the mandibular condyles and the effective biting point leads to a significantly increased biting power in *Coptoformica*. Such a system, however, needs longer adductor contraction distances. The necessary elongation of the whole muscle has led to a posterior extension of occipital corners in *Coptoformica*. This autapomorphy could be a special adaption to nest construction and enables the very effective decapitation of enemy ants and powerful disintegration of food items as e.g., large Lumbricidae.

All queens of *Coptoformica* cannot found new nests independently in a claustral or semiclaustral way. The initial step of colonizing a new site is single queen (flight) dispersal with subsequent socially parasitic colony foundation in host species of the subgenus *Serviformica* Forel, 1913. Except for *Formica (Coptoformica) forsslundi* that seems to have *Formica (Serviformica) transcaucasica* as exclusive host in all parts of its geographic range, distributional data demand that most *Coptoformica* species are not strictly host specific. There are observations suggesting how single queens of ei-

ther *Formica (Coptoformica) pressilabris* or *foreli* (species identity unclear) can found new colonies (Kutter 1969). They go to a nest entrance of a *Serviformica* species, adopt a nymphal posture, and are carried by a host worker into the nest without being attacked or mutilated.

TREATMENT BY SPECIES

Each species section is headed by a synonymic list. The sources from which the identity and synonymy of a taxon was concluded are given in square brackets. These may be direct investigation of type specimens, reasonably clear original descriptions or reasonably clear later descriptions of type material by revising authors. Taxa whose types were not available and whose descriptions are ambiguous were excluded from the synonymic lists and are treated as *incertae sedis*.

To indicate the representation of different geographic areas in the studied material, the countries of origin are given followed by the sum of *morphometrically investigated* specimens of either caste. To clearly define verbal statements in the descriptions, their numeric expression is given in brackets (arithmetic mean \pm standard deviation, minimum-maximum).

Formica exsecta Nylander, 1846

Formica exsecta Nylander, 1846

TYPE LOCALITY. — Helsinki, Finland.

TYPE MATERIAL. — Syntypes 1 male, 1 female, 3 workers (FMNH) [investigated].

Formica exsectopressilabris Forel, 1874. Synonym.

TYPE LOCALITY. — Samedan, Switzerland.

TYPE MATERIAL. — Lectotype 1 queen (designated by Agosti 1989); paralectotypes 2 queens (MHN) [investigated].

Formica exsecta var. *rubens* Forel, 1874. Synonym.

TYPE LOCALITY. — Apples V. Fermaur, Switzerland.

TYPE MATERIAL. — Syntypes 4 workers (MHN) [investigated].

Formica exsecta var. *etrusca* Emery, 1909. Synonym.

TYPE LOCALITY. — Praccia, Italy.

TYPE MATERIAL. — Syntypes 4 workers (MCSN), 1 worker (NHM Basel) [investigated].

Formica daleqi Bondroit, 1918. Synonym. [Synonym; study of topotypical material and description of topotypical population by Agosti (1989)].

TYPE LOCALITY. — Mt Canigou, S France.

TYPE MATERIAL. — Syntypes 3 workers (probably in MNHN), not seen.

Formica exsecta var. *sudetica* Scholz, 1924. Synonym.

TYPE LOCALITY. — Sudety, SE Poland.

TYPE MATERIAL. — Syntypes 1 worker (ZMHU), not seen [type description of Agosti (1989)].

Formica kontunimii Betrem, 1954. Synonym.

TYPE LOCALITY. — Inari, N Finland.

TYPE MATERIAL. — Syntypes not traceable (RNH) [investigation of topotypical material].

Formica nemoralis Dlussky, 1964. New synonym.

TYPE LOCALITY. — Voronesh Reservat, S Russia.

TYPE MATERIAL. — Paratypes 9 workers (ZMLU) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 220 workers, 71 queens, and 22 males came from Norway 5, Sweden 48, Finland 37, Denmark 2, the Netherlands 3, Germany 49, Poland 11, France 5, Switzerland 77, Austria 37, Spain 4, Italy 12, Slovenia 4, Bulgaria 6, Turkey 2, Russia 6, and NE China 5. Total number of specimens seen > 1700.

DESCRIPTION

Worker (Figs 2; 10)

Maximum size larger than in other species (CL 1419 ± 82 , 1200-1641; CW 1362 ± 83 , 1131-1574). Head shape of average *Coptoformica* type (CL/CW 1.042 ± 0.023 , 0.979-1.099); however, long-headed and short-headed specimens may occur within the same nest. Rather long scape (SL/CL 1.008 ± 0.022 , 0.931-1.063). Clypeus at least in anterior third, but normally also in median and posterior portions with standing setae (ClySet 3.54 ± 1.08 , 2-5). Lateral semierect setae in the ocellar triangle usually present (OceSet 92%). Eye hairs at least in a fraction of the nest population strongly developed, often hook-shaped (EyeHL 27.0 ± 6.5 , 0-45; Fig. 10). Pubescence in the ocellar triangle frequently dilute, but enormous intraspecific and intranidal variation occurs (sqrtPDF 5.69 ± 0.90 , 3.78-9.30). Region of occipital corners with semierect to subdecumbent pubescence (however, in specimens of the *etrusca* population almost appressed). Craniad profile of forecoxae with semierect setae

(nCOXA 8.86 ± 3.89 , 0.5-23). Dorsal mesosoma and propodeum occasionally with few standing setae, lateral metapleuron and ventrolateral propodeum more frequently setaceous (nMET 1.86 ± 2.11 , 0-9). Outer edge of the hind tibial flexor side conspicuously hairy (nHTFL 10.97 ± 2.82 , 5.0-23.0), with two size classes of setae, and subdecumbent pubescence (Fig. 2). Semierect setae on gaster tergites as a rule beginning on the 1st tergite (TERG 1.19 ± 0.46 , 1-3); nest sample means of TERG always < 2.4. Pubescence density on first gaster tergite with extreme intranidal and intraspecific variation (sqrtPDG 6.82 ± 1.19 , 3.93-9.88).

Queen

Size definitely larger than in other species (CL 1636 ± 44 , 1514-1741; CW 1721 ± 42 , 1629-1809; ML 2878 ± 116 , 2613-3115). Head broad (CL/CW 0.950 ± 0.022 , 0.900-1.008), scape long (SL/CL 0.956 ± 0.023 , 0.893-1.004). Clypeus at least in anterior third, but normally also in median and posterior portions with standing setae. Lateral semierect setae in the ocellar triangle normally present. Eye hairs normally long and numerous, often hook-shaped (EyeHL 45.6 ± 7.6 , 31-69); samples with less numerous eye hairs may occur. Pubescence in the ocellar triangle relatively dense (sqrtPDF 4.28 ± 0.49 , 3.34-5.75), less variable than in workers. Occipital corners of head normally with semierect smaller setae and pubescence, morphs with almost reduced and such with very developed occipital hairs may occur (OccHD 46.9 ± 22.5 , 7-107). Brilliance of dorsal head surface variable, but relatively matt and weakly sculptured surfaces dominate (GLANZ 1.71 ± 0.36 , 1.0-2.5). Craniad profile of forecoxae with semierect setae (nCOXA 12.95 ± 4.09 , 3.5-23.0). Promesonotum normally with standing setae that clearly differ from semierect pubescence, in weakly haired specimens the differentiation between shorter semierect setae and longer semierect pubescence can be lost (MnHL 181.8 ± 40.0 , 0-256). Outer edge of the hind tibial flexor side conspicuously hairy (nHTFL 12.81 ± 3.20 , 8.0-22.0), with two size classes of setae and subdecumbent pubescence.

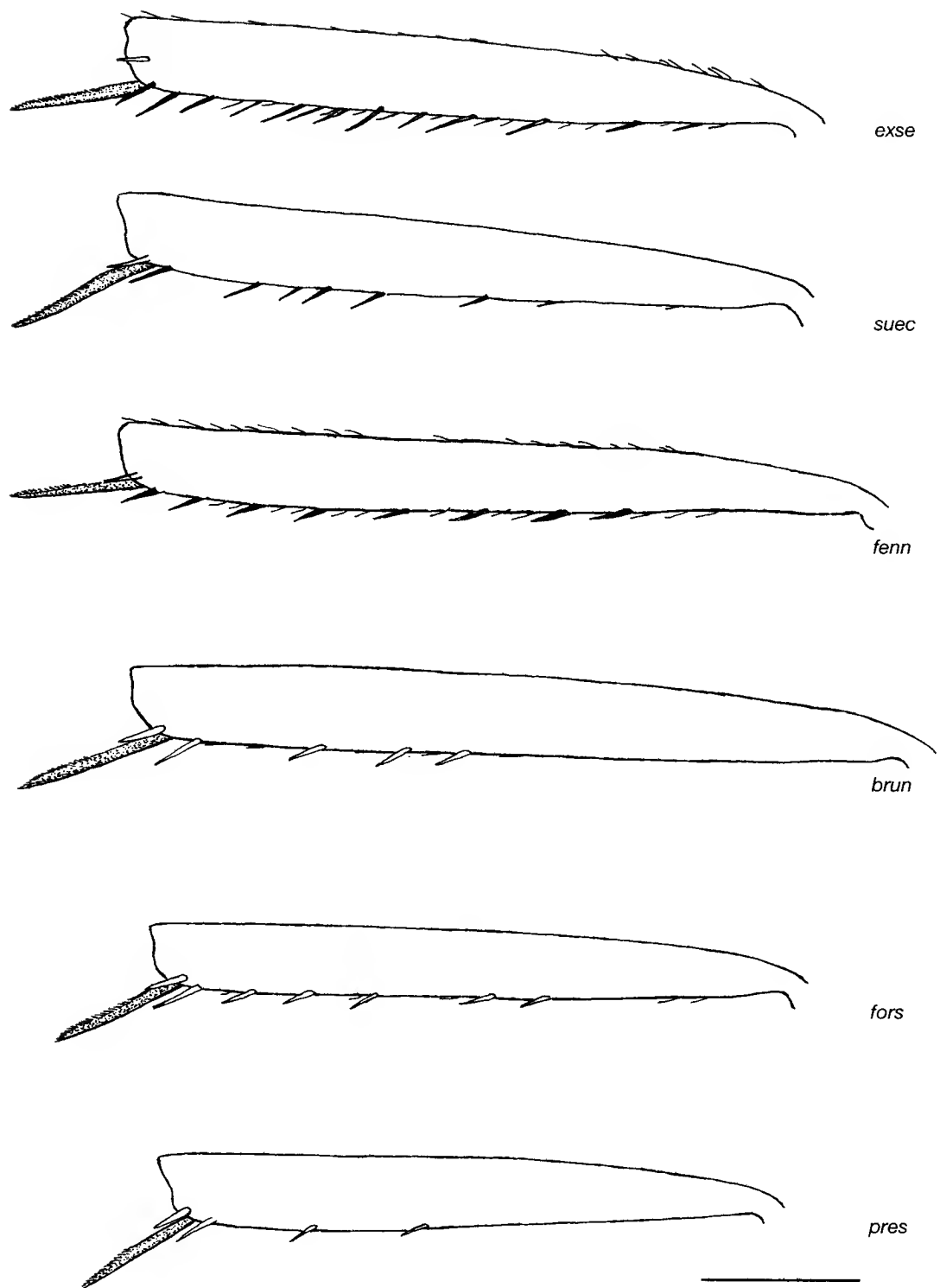


FIG. 2. — Hind tibiae in workers of *Formica exsecta*, *suecica*, *fennica*, *bruni*, *forsslundi*, and *pressilabris*. The view is not fully directed on the large tibial diameter; there is a slight tilt for better visualisation of setae on outer margin of flexor profile. Scale bar: 400 μ m.

Semierect setae on gaster tergites always beginning on the first tergite (TERG 1.00 ± 0.00). Pubescence density on first gaster tergite with extreme intraspecific variation (sqrtPDG 6.17 ± 1.16 , 3.83-9.25).

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

Interspecific setae and pubescence differences between *Coptoformica* species are normally correlated with differences in body measures and indices at least in the queens. Investigations of the enormous setal and pubescence variability of the *exsecta* samples seen during this study could not convincingly show such correlations and could not satisfactorily separate entities of possible taxonomic significance. The same local population may show a wide range of pubescence and pilosity variance and there is no clear indication that certain setae morphs could be associated with a certain distribution, habitat selection, or biology. As a consequence and in agreement with the view of Agosti (1989), *Formica exsecta* is considered here as polymorphic, relatively eurytopic species with a large range, similar to the situation in *Formica truncorum*, *pratensis*, and Scandinavian *lugubris*. This conception of *F. exsecta* contrasts the situation in the other *Coptoformica* species that are constant, monomorphic entities with a defined zoogeography and more specific habitat selection.

Three queen syntypes of *Formica exsecta* var. *exsectopressilabris* Forel, 1874 stored in MHN and labelled "*F. exsectopressilabris* f *Samedan*" are very close to the European population mean of *exsecta* in almost all characters except for subaverage scape length and more developed coxal setae. Their sample means are: CL 1620, CW 1714, ML 2870, CL/CW 0.945, SL/CL 0.922, EyeHL 40.3, GLANZ 1.87, OCCHD 66.0, MnHL 158.0, nCOXA 18.7, TERG 1.0, nHTFL 11.0, sqrtPDF 4.74, sqrtPDG 6.23. Their synonymy is not in question.

Four worker syntypes of *Formica exsecta* var. *rubens* Forel, 1874, stored in MHN and labelled "*exsecta*(M) variét ? (Forel) avec esclav *fusca* V. Fermaur \ *V. rubens* Forel" are rather large,

have subaverage setae numbers, higher TERG, and a more developed reddish pigmentation. These characters, however, are within the range known for *exsecta*, the overall resemblance is too large, and a synonymy is most probable as the following sample means show: CL 1560, CW 1478, SL/CL 0.997, CL/CW 1.056, EyeHL 33.8, TERG 2.3, nCOXA 3.2, nHTFL 8.75, nMET 0.12, sqrtPDF 6.58, sqrtPDG 7.99, Clyset 2.5, OceSet 0.50.

Five worker syntypes (four in MCSN and one in NHM Basel) of *Formica exsecta* var. *etrusca* Emery, 1909, all with locality label "*Praccia VII.90 S.*", deviate from the *exsecta* standard in having a much lower gastral and frontal pubescence distance and an almost appressed pubescence at the occipital corners. Three samples with 12 workers from the terra typica in the Toscanese Alps (from Praccia, Abetone, and Giulia) have the following data (mean \pm SD): CL 1491 ± 116 , CW 1430 ± 112 , SL/CL 1.002 ± 0.020 , CL/CW 1.043 ± 0.009 , EyeHL 33.8 ± 4.3 , TERG 1.00 ± 0 , nCOXA 5.88 ± 3.28 , nHTFL 8.16 ± 2.00 , nMET 0.25 ± 0.40 , sqrtPDF 4.85 ± 0.71 , sqrtPDG 4.74 ± 0.86 , ClySet 2.50 ± 0.80 , ClyPub 4.12 ± 0.96 , OceSet 92%. The mean values of sqrtPDG, sqrt PDH, and EyeHL of the population from the Toscanese Alps significantly differ from those of the *exsecta* population from outside this region ($p < 0.001$). *Etrusca* is assumed here to represent a deviating local population of *exsecta*. A more extensive population study and search for diagnostic genetic markers are needed to test if *etrusca* already represents a separate evolutionary line worth to carry a taxonomic name. The high phenotypic similarity between *etrusca* and *mesasiatica* Dlussky should be considered in such an investigation.

Type specimens of *Formica dalcqi* Bondroit, 1918 (type locality: Mt Canigou /E Pyrénées, 1 800 m) were not studied. However, three topotypical workers in NHM Basel, labelled "*Canigou 2200 m, Pyrénées or. Weill.*" were available and had the following sample means: CL 1392, CW 1385, SL/CL 1.015, CL/CW 1.005, EyeHL 27.0, TERG 1.0, nCOXA 10.0,

nHTFL 11.5, nMET 0.7, sqrtPDF 5.46, sqrtPDG 7.41, Clyset 4.0, ClyPub 3.0, Oceset 100%. All these data are within the usual range of variation known for *exsecta*. Agosti (1989) studied the population at the locus typicus and stated that all characters presented by Bondroit as diagnostic for *dalcqi* were variable in this population as they were in *exsecta* in general. As a consequence there is no suggestion for a heterospecificity of *dalcqi*.

The type worker of *Formica exsecta* var. *sudetica* Scholz, 1924 from the Sudety mountains / SW Poland was not seen. The pigmentation characters presented by Scholz (1924) as characteristic for this form are not known to have a diagnostic value in any known species and also habitat selection, nest construction, polycaly, and aggressive behaviour do not show deviations from the *exsecta* standard. Agosti (1989) examined the type specimen and stated that the sculpture characters presented by Scholz for *sudetica* ("the usually rather expressed longitudinal carina and lateral longitudinal carinulae of the propodeum") may also occur in other populations. Hence, the synonymisation of *sudetica* is most probable.

The type specimens of *Formica kontuniemii* Betrem, 1954 from Inari / N Finland are not traceable in the Museum of Leiden (Agosti 1989). As diagnostic characters of this very hairy form were presented by Betrem (1954) the presence of standing setae on gula, prosternum, pronotum, and propodeum. The sympatric occurrence of very hairy forms matching the description of *kontuniemi* and of less hairy forms was observed by the author throughout Fennoscandia (see also Agosti 1989) and a distinct cluster of very hairy ants could not be demonstrated by discriminant functions in the studied material. Thus, the synonymy of *kontuniemi* with *exsecta* seems most probable though the problem should be investigated with more sophisticated methods.

Nine paratype workers of *Formica nemoralis* Dlussky in the collection of ZMLSU, collected from the same colony as the holotype, and labelled "Voron.Sap. 29.VII.1962 No 221 Dlussky" are in any character within the range of variability

known for nest sample means of *exsecta* and are almost identical with the type workers of *rubens*. Six measured paratype workers of *nemoralis* had the following mean values (in brackets the means of the *rubens* types): CL 1360 (1560), CL/CW 1.057 (1.057), SL/CL 0.977 (0.997), EyeHL 27.5 (33.8), TERG 2.17 (2.33), nCOXA 3.2 (3.2), nHTFL 7.5 (8.5), nMET 0.0 (0.1), sqrtPDF 6.53 (6.58), sqrtPDG 7.77 (7.99), Clyset 2.5 (2.5), ClyPub 3.1 (no data), Oceset 0.83 (0.50). The rather low TERG value in the *nemoralis* types is explained by an abnormal reduction of setae on first and second gaster tergite in one portion of the specimens, possibly caused by a mutation. Queen types of *nemoralis* were not available to the author, but descriptions of females from this colony (Dlussky & Pisarski 1971; Agosti 1989) give some diagnostic characters. The queens have a dark, shining body surface (according to Agosti within the range known for *exsecta*) and their metric measures are equal to the means known for *exsecta*. As average of the data of Agosti, Pisarski, and Dlussky is calculated a thoracic length of 2900, an overall head length of 1920, a CW of 1690, and a SL of 1600. As a consequence, *Formica nemoralis* should represent a less hairy morph of *exsecta* and should be kept in synonymy.

BIOLOGY AND DISTRIBUTION

Geographic range

South to Central Spain, to the N Appennine and to the Balkans at 40°N. Found in high Anatolia and Caucasus; apparently absent from the driest Pontic and Caspian steppe zones. West to SW England and the Scottish Highlands. Northern range throughout Fennoscandia up to North Cape. Distribution in the east in European Russia, across Siberia, Mongolia, NE China (Beishan National Park, 37°N, 102°E) and east to the lower Amur river. The northern distribution in the continental parts of Eurasia is limited by the - 8 °C isotherm of soil in a depth of one meter (achieved at 67°N in W Siberia at the Ob river and at 62°N in E Siberia at the Lena river) and the southern distribution coincides with the southern border of forest-steppe (Dlussky 1967). Vertical distribution: in

Switzerland and Austria 300-2250 m, bimodal, with very low frequencies from 800-1200 m; Bulgarian mountains 1100-2200 m.

Habitat selection

F. exsecta is more a generalist with a wider habitat selection than usual within *Coptoformica* species. Very different open or slightly shaded habitats, which must have medium-term stability at least, are inhabited. A high cover percentage of grasses within the field layer is typical but not essential. As for all species of the group, sites with rapid plant succession, with high nitrogen input, or sites within the inundation plains of rivers are not colonised. *Formica exsecta* and all other members of the group cannot increase nest temperatures by metabolic heat production independent of environmental temperatures as known for populous nests of some wood ant species. The dependence of *Coptoformica* upon direct insolation is thus increased and nests cannot be constructed in fully shaded woodland habitats. Habitat types used by *exsecta* are subalpine and boreomontane pastures, clearings and margins of woodland, sunny forests, semidry to xerothermous grasslands, heathland, and dryer spots of bogs and fens.

Status as threatened species

Red List Germany: three (threatened). In Central Europe it is probably the least endangered *Coptoformica* species though its populations have significantly declined since 1950. The decline is caused by afforestation of clearings and meadows, vanishing of coppice wood management, decline of sheep pasturing, intensifying of cattle pasturing, intensive use of mineral fertilisers and liquid manure, and high atmospheric nitrogen immision. Dewes (1993) recorded *F. exsecta* colonies in the Nature Park Saar-Hunsrück preferentially in sites of historic coppice wood management where oak bark for tanneries was harvested.

Colony foundation

Flight or ground dispersal of single queens is followed by socially parasitic colony foundation in nests of the subgenus *Serviformica*. *Formica fusca* (Dlussky, Collingwood, Pisarski, Agosti, Seifert)

and *Formica lemani* (Collingwood, Agosti, Hellrigl, Seifert) are reported as host species. According to Pisarski (1982), socially parasitic colony foundation is only possible in queenless host nests. The same author stated that monogynous nests of *exsecta* never accept alien queens, with exception of very minute nests. To become polygynous, they must have lost the queen and can then adopt several queens simultaneously. Once shifted to polygyny, huge polycalic colony systems may develop by nest splitting.

Nest construction

Nest mounds are often more structured than in related species. Materials and type of nest construction depend upon insolation, ground water level, soil type, and composition of vegetation. The following type is frequent on mineralic soils: a calotte-like outer hull of the dome, which can often be lifted without breaking (Agosti 1989), is constructed with more dense, strongly adhesive materials (usually finely cut grass pieces). Rather voluminous upper brood chambers (during warm weather the sites for pupae) may be situated between this hull and inner mound material that consists of more lofty plant pieces. The lower mound core is a mixture of humified plant material and mineralic soil. Galleries may reach 150 cm down into the soil. In polygynous nests and during summer, numerous clearly separated chambers of 2 cm width are found below the level of soil surface down to 80 cm. These chambers usually contain a queen, eggs, small larvae, and few workers. In habitats deficient of grasses, other materials as coniferous needles, rabbit pellets, or small pebbles may be used. Nest diameters may reach 200 or even 300 cm (Agosti 1989; Dlussky 1967). In semi-shaded boreal forests, the author observed nest mounds of 150 cm height and 180 cm diameter, the base of which had been abandoned by the ants and covered by mosses (*Polytrichum*).

Development and microclimatic requirements

Alates develop from eggs laid in early spring. Oviposition starts in Central European lowland

habitats in late March but is considerably delayed with growing altitude and latitude. In Finnish monogynous colonies, less than 5% of the spring eggs develop to workers (Chapuisat *et al.* 1997), but this ratio may reach 50% in Swiss polygynous societies (Schneider pers. comm.). The main source of worker production is late spring or summer eggs. The optimum temperature for "brood development" is 28–30 °C (Grinfeld 1939, cited in Dlussky 1967). The supercooling point of winter-adapted Siberian workers is -20 °C; the long-term minimum at which 50% of workers survive is -8 °C (Berman, Shigulskaja & Leirich 1987; Leirich 1989). The conditions where soil temperatures in a depth of one metre do not decline below -8 °C are given in E Siberia up to 62°N, which coincides with the northern distributional border of *exsecta*.

Demography of nests and colonies

The ratio of monogynous nests *vs* polygynous/polycalic colonies differs locally and geographically. Patchiness and general availability of suitable habitats and a payoff between the costs of single queen colony foundation and the costs of reproductive competition in polygynous nests are probable factors influencing this ratio. In S Finland monogyny/monodomy clearly predominates. Big polycalic colonies are known from the Alps, Central Europe, and European Russia. The mean longevity of queens in monogynous nests in S Finland was over 20 years (Pamilo 1991). According to Sundström *et al.* (1996), 39% of the queens in 57 monogynous S Finnish nests were multiply-mated (polyandrous). The sex ratio of produced alates is strongly dependent upon the number of queens in a colony and the number of mates per queen; in highly polycalic colonies in the Swiss Alps it was about 15 : 1 (Schneider pers. comm.), in Finnish polyandrous/monogynous colonies it was 3.76 : 1, but in Finnish monoandrous/monogynous nests it was 1 : 2.2. Workers of the latter colonies increased their inclusive fitness by selectively killing male larvae before pupation and (most probably) feeding them to the now rapidly growing female larvae. Ecological and demographic factors

(recourse limitation!) are believed to interfere with genetic factors (optimisation of kinship value), i.e. males should survive in higher numbers in monoandrous/monogynous nests if there is plenty of resources (Chapuisat *et al.* 1997). Monogynous nests mainly produce the large male morph (macraner) but polycalic colonies mainly micraners (Pamilo & Rosengren 1984). The micraners can develop from worker-laid eggs, mature later, and show narrower activity peaks. Both micraners and macraners are normally haploid (Agosti 1989).

No complete population census has been performed so far in *exsecta*. The "Aussendienst" population of four monogynous nests of 368 ± 100 cm² basal area was censused by Pisarski (1982) as 2750 ± 1000 workers, i.e. 7.5 workers/cm² basal nest area. That means a total population of 18.8 workers/cm² basal nest area if assuming 40% Aussendienst workers. The total population of exactly censused polygynous *bruni* nests was 39.3 workers/cm² basal nest area (Schneider pers. comm.). Both values seem realistic in view of the higher worker density and smaller worker size in polygynous nests. A very large polygynous *exsecta* nest of 150 cm diameter should then contain > 300 000 workers. Polycalic *exsecta* colonies may be huge and can dominate a site as known for *polycena*. Dewes (1993) described a supercolony comprising 408 nests (the smallest not counted!) spreading over an area of 2 ha. If assuming only 25 000 workers for an average polygynous *exsecta* nest, the whole population of this colony should be > 10 000 000.

Swarming

Mature alates are found in the nest 28.2 July \pm 20.2 d (10 June–4 Sept, $n = 33$). In contrast to R. Rosengren, M. A. Schneider did not observe micraners to fly higher and farther than macraners. In Swiss polycalic colonies about 30% of females fly, the others are inseminated at the nest mounds. Swarming is restricted to the first half of the day (between 5.30 and 12.20 h) and starts as soon as the first direct sunlight hits the mound surface. Completely cloudy sky or strong air movement prevents the flight and beginning

sunshine in the second half of the day can not release it (Schneider pers. comm., and my own observations).

Food sources

F. exsecta can use a wide range of food sources. Trophobiosis with epigeic and subterranean Aphidina (and more rarely Cicadina and Coccina) is observed and obviously covers a major portion of the energy needs. Lachnidae are the main trophobionts in coniferous and deciduous forests. Zoophagy may be important and is then comparable to that of *Formica polyctena* with the difference of a smaller average size of prey items (Wesselinov & Horstmann 1968); all kinds of dead or living Arthropoda and Lumbricidae are consumed. Very populous supercolonies effectively displace different species of predatory arthropods from their territory.

Intraspecific behaviour

Monogynous colonies are highly aggressive against conspecific aliens. Polygynous/monodomous colonies show reduced aggressivity but only polycalic colonies do not establish territorial boundaries against other conspecific polycalic colonies (Pisarski 1982).

Formica mesasiatica Dlussky, 1964

TYPE LOCALITY. — Talasskiy Alatau and Zailiyskiy Alatau, Tyanshan.

TYPE MATERIAL. — Paratype (MZ).

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — Numerically evaluated were 11 different samples with 18 workers and 8 queens from the Tyanshan mountains of S Kazakhstan (7) and Kyrgyzstan (19). Total number of specimens seen 70.

DESCRIPTION

Worker

Very large (CL 1468 ± 61 , 1359-1582; CW 1414 ± 61 , 1321-1535). Head shape as in *exsecta* (CL/CW 1.038 ± 0.014 , 1.002-1.061). Scape long (SL/CL 1.027 ± 0.019 , 0.989-1.059). Clypeus also in median and posterior portions with standing setae (ClySet 4.22 ± 0.43 , 4-5).

Lateral semierect setae in the ocellar triangle always present (OceSet 100%). Eye hairs always strongly developed, often hook-shaped (EyeHL 35.7 ± 4.6 , 30-47). Pubescence in the ocellar triangle always very dense (sqrtPDF 3.99 ± 0.22 , 3.58-4.41). Occipital corners in contrast to the *exsecta* standard with almost appressed pubescence. Craniad profile of forecoxae with few semierect setae (nCOXA 4.58 ± 0.90 , 3.0-5.5). Dorsal pronotum and propodeum occasionally, lateral metapleuron and ventrolateral propodeum always with few standing setae (nMET 3.61 ± 1.26 , 1.5-6.0). Outer edge of hind tibial flexor side conspicuously hairy (nHTFL 9.50 ± 0.99 , 8.0-11.0), with two size classes of setae, and subdecumbent pubescence. Semierect setae on gaster tergites beginning on the first tergite (TERG 1.00 ± 0.0). Pubescence distance on first gaster tergite very low (sqrtPDG 4.43 ± 0.65 , 3.72-6.14).

Queen

As large as *exsecta* (CL 1642 ± 33 , 1585-1687; CW 1721 ± 22 , 1697-1765; ML 2949 ± 79 , 2831-3040). Head broad (CL/CW 0.955 ± 0.023 , 0.926-0.985), scape significantly longer than in *exsecta* (SL/CL 0.994 ± 0.023 , 0.957-1.024). Clypeus also in posterior portions with standing setae. Lateral semierect setae in the ocellar triangle usually present. Eye hairs always long and numerous, often hook-shaped (EyeHL 49.2 ± 6.2 , 40-55). Pubescence in the ocellar triangle always very dense (sqrtPDF 3.56 ± 0.20 , 3.33-3.85). Occipital corners of head with decumbent or subdecumbent hairs (OccHD 38.5 ± 9.3 , 31-59); queens with appressed hairs are reported to occur (Dlussky 1967). Brilliance of dorsal head surface low, weakly sculptured surfaces dominate (GLANZ 1.41 ± 0.38 , 1.0-2.0). Craniad profile of forecoxae with semierect setae (nCOXA 8.06 ± 1.52 , 6.0-11.0). Promesonotum always with standing setae that clearly differ from semierect pubescence (MnHL 195.3 ± 29.2 , 152-233). Outer edge of the hind tibial flexor side conspicuously hairy (nHTFL 9.43 ± 2.87 , 6.0-15.0), with two size classes of setae and subdecumbent pubescence. Semierect setae on gaster

tergites always beginning on the first tergite (TERG 1.00 ± 0.00). Pubescence distance on first gaster tergite constantly very low (sqrtPDG 3.56 ± 0.20 , 3.33-3.85).

TAXONOMIC COMMENTS AND

DIFFERENTIAL DIAGNOSIS

Formica mesasiatica is so far the only reported *Coptoformica* species from Middle Asia (Tyanshan and N Pamir). This population seems to be fully isolated from the Palaearctic range of *exsecta*. The description presented here is based upon investigation of a paratype queen stored in MZ, labelled: "Zailiyskij Ala-Tau, verch. r. Almatin, 18.7.58" and the investigation of further 10 samples with workers and queens collected by R. Schultz in the Kazakhian and Kyrgyzian Tyanshan. *F. mesasiatica* shows highly significant ($p < 0.0001$) differences to *exsecta* in sqrtPDG, sqrtPDH, and nCOXA of queens and workers and in SL/CL of queens (Tables 6; 8). However, it cannot be completely separated from *exsecta* by discriminant functions even on the basis of nest sample means. Because of the very peculiar zoogeographic situation *mesasiatica* is treated here as species. Complete isolation and bottle-necking events could have caused a loss in phenotype diversity.

BIOLOGY AND DISTRIBUTION

The distribution is apparently limited to the mountain areas of the Tyanshan and N Pamir where the species is found on steppe-like or semi-dry grasslands and woodland clearings between 1300-2700 m (Dlussky 1967; Tarbinsky 1976; Schultz pers. comm.). The highest densities were observed in grasslands with bushes. Monodomous nests as well as polycalic colonies were observed. Nuptial flights are delayed with growing elevation and were observed between June 29 and July 30.

Formica fukaii Wheeler, 1914

Formica exsecta var. *fukaii* Wheeler, 1914

TYPE LOCALITY. — Saitama, Japan.

TYPE MATERIAL. — Syntypes 4 workers (MCZ) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — Numerically evaluated were five different samples with 12 workers and one queen from Japan.

DESCRIPTION

Worker

Very large (CL 1481 ± 40 , 1418-1548; CW 1413 ± 49 , 1343-1486). Head shape similar to *exsecta* (CL/CW 1.048 ± 0.012 , 1.025-1.063). Scape very long (SL/CL 1.046 ± 0.018 , 1.018-1.071). Standing setae on clypeus restricted to the anterior part (ClySet 1.83 ± 0.39 , 1-2). Lateral semierect setae in the ocellar triangle rarely present (OceSet 33%). Eye hairs always strongly developed (EyeHL 28.5 ± 2.8 , 25-34). Pubescence in the ocellar triangle always very dense (sqrtPDF 4.02 ± 0.31 , 3.65-4.90). Craniad profile of forecoxae only exceptionally with single apical setae (nCOXA 0.08 ± 0.29 , 0-1). Lateral metapleuron and ventrolateral propodeum without standing setae (nMET 0.0 ± 0.0). Outer edge of the hind tibial flexor side hairy (nHTFL 7.20 ± 2.33 , 1.0-10.0). First gaster tergite always without standing setae (TERG 2.75 ± 0.45 , 2-3). Pubescence distance on first gaster tergite extremely low (sqrtPDG 3.93 ± 0.13 , 3.68-4.16).

Queen

Very large (CL 1672, CW 1707, ML 2948). Head broad (CL/CW 0.979), scape long (SL/CL 0.967). Clypeus only in anterior part with setae. Lateral semierect setae in the ocellar triangle absent. Eye hairs long and numerous (EyeHL 46). Pubescence in the ocellar triangle extremely dense (sqrtPDF 3.11). Occipital corners of head only with short decumbent hairs (OccHD 15). Brilliance of dorsal head surface intermediate (GLANZ 2.0). Craniad profile of forecoxae without or only single apical setae (nCOXA 0-1). Promesonotum without standing setae (MnHL 0). Outer edge of the hind tibial flexor side with several setae (nHTFL 7.0). Semierect setae on gaster tergites beginning on the third tergite (TERG 3.0). Pubescence distance on first gaster tergite extremely low (sqrtPDG 3.23).

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

All Japanese material, including four worker syntypes from MCZ Cambridge, labelled “*Saitama, Japan Formica exsecta* var. *fukai* Syntypes, MCZ Cotype 23247”, clearly differs from *exsecta* and *mesasiatica* by constant absence of setae from first (workers) or first and second gaster tergites (queens), by the reduced coxal pilosity, by the complete reduction of setae in median and caudal parts of clypeus, and by the frequent reduction of setae in the ocellar region. The frontal and gastral pubescence distance is extremely low in both workers and queens and achieves in the latter caste values not found in other species. Agosti gave as pubescence density on median part of second gaster tergite 2295 hairs/mm² for a *fukai* queen but only 1348 hairs/mm² as upper extreme for eight measured *exsecta* queens. The complete reduction of standing promesonotal setae in the *fukai* queens is another differential character. Hence, there is little doubt that *fukai* represents an endemic Japanese species. It is distributed there between 35 and 44°N. The synonymisation of *fukai* with *mesasiatica* as performed by Sonobe & Dlussky (1977) is clearly contradicted by setae counts and setae positions. These authors also gave some notes on the ecology of *fukai*.

Formica manchu Wheeler, 1929

Formica exsecta var. *manchu* Wheeler, 1929

TYPE LOCALITY. — Manchuria: Boketu (= Buchatu = P'o-k'o-r'u; 48°45'N, 121°58'E).

TYPE MATERIAL. — Syntypes 9 workers (MCZ) [investigated].

Formica dluskyi Bolton, 1995 (replacement name for *longiceps* Dlussky, 1964, a junior primary homonym of *longiceps* Smith, 1863). Synonym.

TYPE LOCALITY. — S Central and E Siberia.

TYPE MATERIAL. — Paratypes 4 workers (NHM Basel and ZIPAS) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 34 workers came from Mongolia (2 samples), N Tibet (4 samples), and Manchuria (1 sample). Total number of specimens seen 50.

DESCRIPTION

Worker (Figs 17; 18)

Medium-sized species (CL 1375 ± 76, 1193–1542; CW 1282 ± 71, 1128–1458). Head significantly longer than in other species (CL/CW 1.067 ± 0.016, 1.036–1.103). Scape rather long (SL/CL 1.013 ± 0.018, 0.966–1.048). Setae only present on anterior clypeus (ClySet 1.67 ± 0.56, 1–3). Lateral semierect setae in the ocellar triangle rarely present (OceSet 12%). Eye hairs strongly developed (EyeHL 27.9 ± 6.8, 12–29). Pubescence distance in the ocellar triangle large (sqrtPDF 5.95 ± 0.50, 4.95–6.92). Craniad profile of forecoxae without or very few subdecumbent setae (nCOXA 1.30 ± 0.91, 0–3.5). Dorsal mesosoma, lateral metapleuron and ventrolateral propodeum only exceptionally with single standing setae (nMET 0.04 ± 0.26, 0–1.5). Outer edge of the hind tibial flexor side with subdecumbent setae (nHTFL 4.78 ± 1.90, 1.0–9.0). Semierect setae on gaster tergites beginning at the posterior border of second to third tergite (TERG 2.91 ± 0.29, 2–3), anterior part of sculptured surface of third tergite always with setae. Pubescence distance on first gaster tergite very large (sqrtPDG 7.57 ± 0.59, 6.46–8.84).

Queen

(Not seen, description according to Agosti 1989): “[...] Clypeus only at the anterior margin with a number of standing setae that have the same length as pubescence hairs. Eyes with standing setae. Head, mesosoma, petiole, and gaster without standing setae [few small setae are most probably present at the hind margin of third or fourth gaster tergite, B. S.], instead a homogeneous, long, subdecumbent pubescence is present. Hind tibiae with long, subdecumbent pubescence. Head surface shagreened with homogeneously scattered, fine, smooth, and shining punctures [...]”. Some morphometric data can be predicted from the average correlations between queen and worker data observed in *Coptoformica* and from transformation of some data of Agosti: ML 2315, CL/CW 1.030, SL/CL 0.960, EyeHL 46, nCOXA 1, TERG 3.5, nHTFL 5.5, sqrtPDF 5.3, sqrt PDG 7.5.

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

The nine syntype workers of *manchu* labelled "Boketu, Manchuria, 7.7.1926" (MCZ) and four paratype workers of *dluskyi* labelled "Baian Davaa, 75 km E Ulan Bator, 6.VI.1962 leg. B. Pisarski No 3350" (NHM Basel and ZIPAS) and "Mongolia: Gorchi 50 km NE Ulan Bator, 25.V.1962, leg. B. Pisarski & R. Bielawski" (MZ) are practically identical in the mean values of their characters (first value *manchu*, second value *dluskyi*): CL/CW 1.075, 1.076; SL/CL 1.023, 1.024; EyeHL 26.8, 27.7; TERG 3.00, 2.75; nHTFL 5.28, 5.00; nMET 0.00, 0.38; sqrtPDF 5.90, 6.20; sqrtPDG 7.52, 7.56; Clyset 1.11, 2.00; and nCOXA 0.36, 2.25. The only significant difference is the lower number of coxal setae in the *manchu* series but such moderate deviations are normal in species with low coxal setae numbers (e.g., *fennica*, *bruni*, *forsslundi*). The weak differences in head shape between the types of *manchu* and *dluskyi* (Figs 17A; 18A) have no significance in view of the considerable intraspecific variability of this character. As a consequence, the high similarity of character combinations and the zoogeographic proximity of the type localities indicate that *dluskyi* most probably represents a junior synonym of *manchu*.

BIOLOGY AND DISTRIBUTION

The samples studied and the site records given by Dlussky (1967) indicate an E Palearctic distribution between 96°E (Kansk) and 130°E (Yakutsk) and 36°N (N Tibet) to 62°N (Yakutsk). Several samples collected by A. Gebauer in a bushy steppe habitat in the Southern Koko Nur Mountains (NE Tibet) in 1990/96 came from polydomous colonies.

Formica fennica n. sp.

TYPE MATERIAL. — 1 queen holotype and 6 worker paratypes are labelled "FIN: 62.07N, 29.48E, road No. 71, Kitee-17W, Puhos-6.5WNW, leg. Seifert 1996.07.13-119"; 1 queen paratype, 5 worker paratypes from the same polycalic colony and same

date but different nest number "FIN...1996.07.13-86"; 3 male paratypes, 6 worker paratypes from the same polycalic colony and same date but different nest number "FIN...1996.07.13-105"; 5 worker paratypes labelled "FIN: 63.27N, 27.10E, Iisalmi-13 km S, Kotikylä, 1998.07 leg. J. Sorvari"; 7 paratype workers labelled "CAU: 42.23N, 45.42E, Schenako, 1600 m, 1985.08.01, 20°N-exp. kurzgrasige Weide". All these mounted type specimens (plus 55 worker paratypes in ethanol) are stored in SMN Goerlitz. In the collection of ZM Turku are stored 1 paratype queen "FIN: 62.07N, 29.48E, road No. 71, Kitee-17W, Puhos-6.5WNW, leg. Seifert 1996.07.13" and 1 worker paratype "FINLAND: Ilomantsi, Maukkula (695: 69)".

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 27 workers, three queens, and three males came from Finland 27 (three localities) and Caucasus 6 (one locality). Total number of specimens seen 90.

DESCRIPTION

Worker (Figs 1F; 2-4; 12)

Medium-sized species (CL 1340 ± 110, 1087-1514; CW 1257 ± 106, 1012-1426). Head with acute and well-pronounced occipital corners (Fig. 1F) and significantly longer than in other European species (CL/CW 1.067 ± 0.016, 1.036-1.103). Scape of average length (SL/CL 0.989 ± 0.021, 0.945-1.035). Setae only present on anterior clypeus (Fig. 3, ClySet 1.67 ± 0.56, 1-3). Lateral semierect setae in the ocellar triangle rarely present (OceSet 22%). Eye hairs strongly developed (EyeHL 23.2 ± 3.1, 17-30). Pubescence hairs in the ocellar triangle long and very sparse (sqrtPDF 6.68 ± 0.67, 5.19-8.19; Figs 4; 12). Craniad profile of forecoxae without or very few subdecumbent setae (nCOXA 0.91 ± 0.83, 0-3). Dorsal mesosoma, lateral metapleuron and ventrolateral propodeum without standing setae (nMET 0.0 ± 0.0). Outer edge of the hind tibial flexor side with well-developed subdecumbent setae and subdecumbent pubescence (Fig. 2, nHTFL 8.13 ± 2.33, 4.0-14.0). Semierect setae on gaster tergites beginning at the posterior border of third to fifth tergite (TERG 3.37 ± 0.56, 3-5), anterior part of third tergite always without setae. Pubescence density on first gaster tergite very low (sqrtPDG 7.89 ± 0.46, 6.99-8.73).

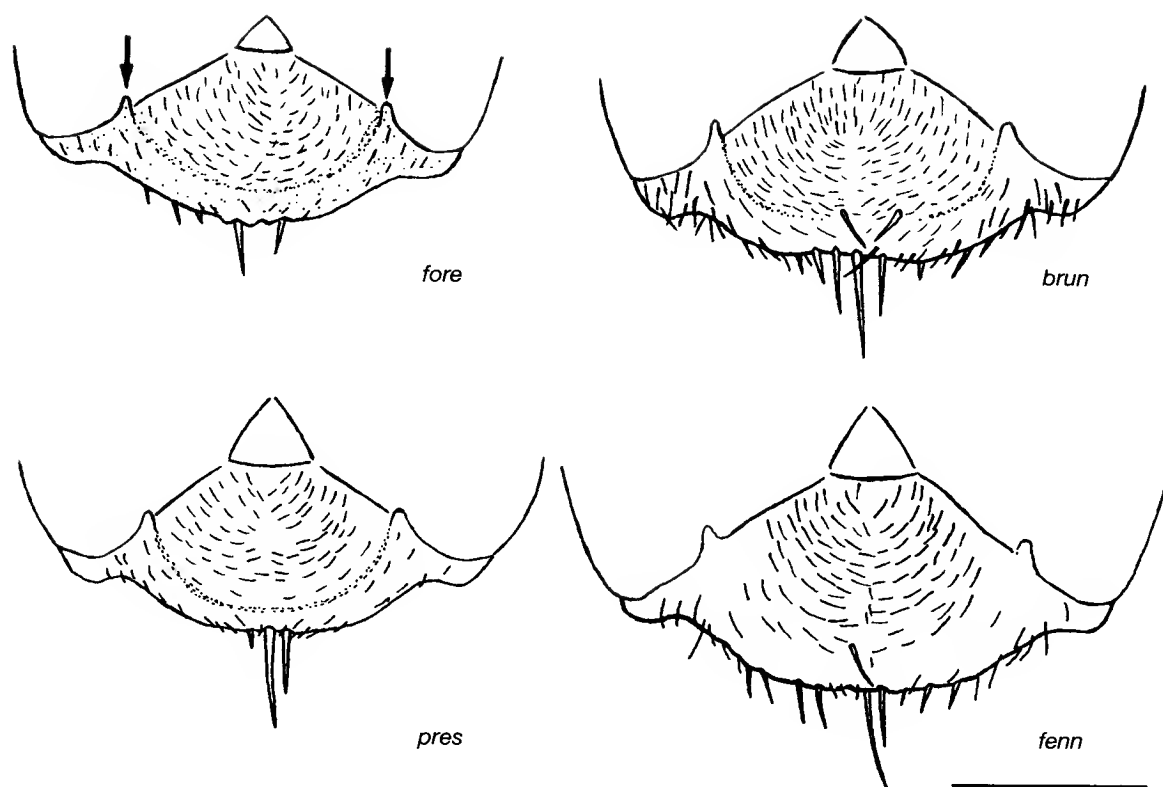


FIG. 3. — Setae and pubescence on clypeus of *Formica foreli*, *brunii*, *pressilabris*, and *fennica*; the arrows in *fore* point to the tentorial pits. Scale bar: 400 μ m.

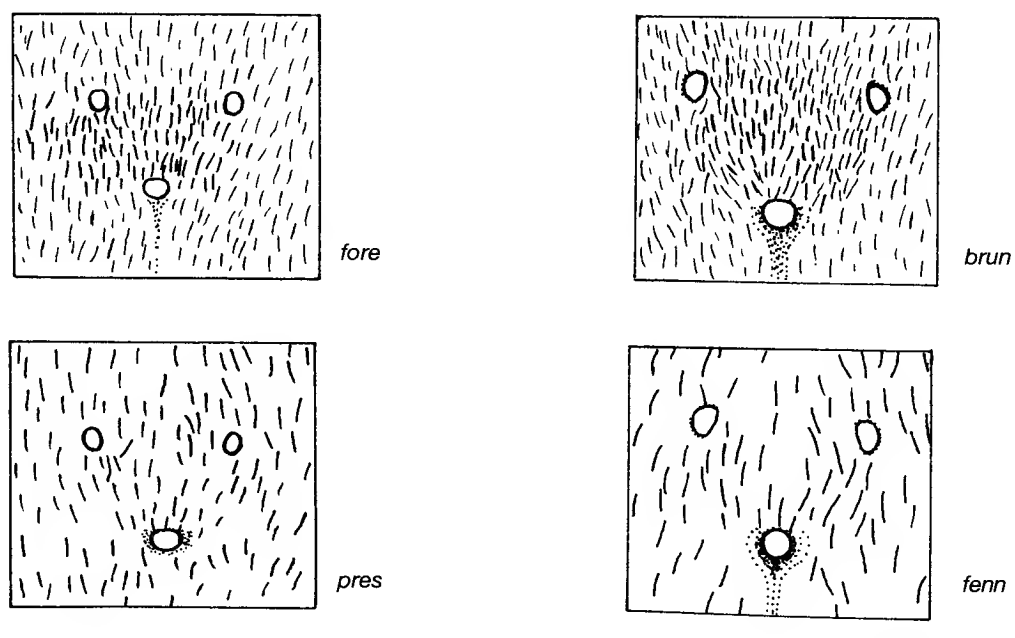


FIG. 4. — Pubescence in the ocellar region of *Formica foreli*, *brunii*, *pressilabris*, and *fennica*. Scale bar: 300 μ m.

Queen (Fig. 5)

Rather large, in size between *exsecta* and *bruni* (CL 1543 ± 47 , 1490-1582; CW 1520 ± 26 , 1492-1544; ML 2611 ± 53 , 2551-2651). Head significantly slender than in *exsecta* (CL/CW 1.015 ± 0.014 , 0.999-1.025), scape of average length (SL/CL 0.918 ± 0.008 , 0.911-0.927). Setae restricted to anterior clypeus (ClySet 1.67 ± 0.58 , 1-2). Clypeus lateral of the tentorial pit level with pubescence hairs surpassing the anterior margin by more than 10 μ m. Lateral semierect setae in the ocellar triangle absent. Eye hairs long (EyeHL 35.3 ± 5.5 , 30-41). Pubescence in the ocellar triangle decumbent, very long, and sparse PDF 6.07 ± 0.73 , 5.55-6.91). Occipital corners of head with long, decumbent to almost appressed pubescence (OccHD 27.7 ± 2.1 , 26-30). Dorsal head surface relatively matt and weakly sculptured (GLANZ 1.33 ± 0.29 , 1.0-1.5). Craniad profile of forecoxae without or very few semierect setae (nCOXA 0.67 ± 0.76 , 0-1.5). Mesonotum with decumbent to appressed pubescence and without real setae (MnHL 63.6 ± 53.2 , 0-97, these are long pubescence hairs). Outer edge of the hind tibial flexor side with numerous subdecumbent setae and long decumbent pubescence (nHTFL 9.50 ± 1.80 , 8.0-11.5). Semierect setae on gaster tergites beginning on the fourth tergite (TERG 4.0 ± 0.0). Pubescence on first gaster tergite long and very sparse (sqrtPDG 8.11 ± 0.81 , 7.47-9.02).

TAXONOMIC COMMENTS AND
DIFFERENTIAL DIAGNOSIS

Close relationship of *F. fennica* to *F. manchu* Wheeler is indicated by the similarity of workers. The two taxa differ from all other Palaearctic *Coptoformica* species by significantly longer heads (CL/CW 1.067-1.073). *F. manchu* and *fennica* further share the character combination of conspicuous eye hairs (mean EyeHL 23-28 μ m), complete absence of setae from first gaster tergite (mean TERG 2.9-3.4), rare occurrence of setae in the ocellar region, and very dilute tergite pubescence (mean sqrtPDG 7.6-7.9).

The *manchu* cluster represented by seven nest samples with 34 workers from Mongolia,

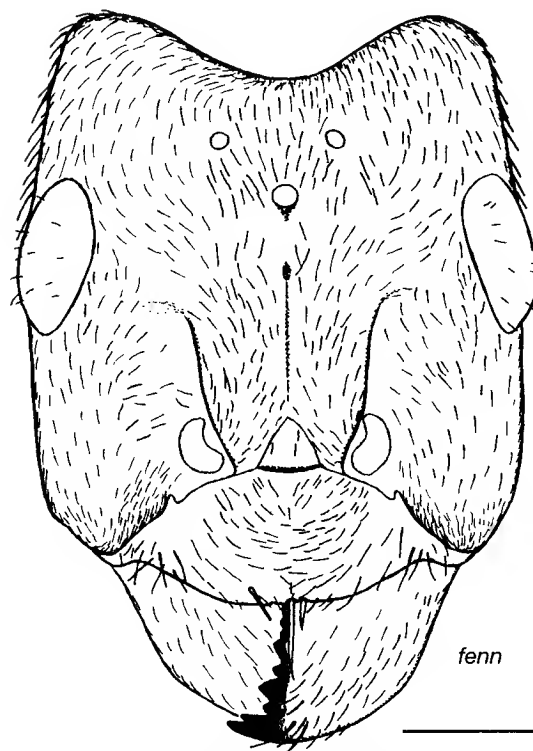


FIG. 5. — Head of the paratype queen of *Formica fennica* from nest No 1996.07.13-86. Scale bar: 400 μ m.

N Tibet, and Manchuria differs from the W Palaearctic *fennica* cluster represented by six nest samples with 27 workers by significantly larger SL/CL ($p < 0.0001$) and by significantly smaller TERG ($p < 0.001$), nHTFL ($p < 0.0001$), and sqrtPDF ($p < 0.0001$). The *manchu* workers constantly show an additional set of conspicuous setae in the anterior portion of the sculptured surface of third tergite and the setae on outer hind tibial flexor margin are shorter, finer, and less numerous than in *fennica* (compare Figs 2, 17C and 18C). In the *fennica* workers, setae may be present at the caudal margin of third tergite but never in the anterior portion of the sculptured surface of third tergite. A numeric separation of the *fennica* and *manchu* workers is possible with by a linear discriminant score $D(4)$ calculated as $D(4) = 0.155 \text{ sqrtPDF} + 0.134 \text{ TERG} + 0.064 \text{ nHTFL} - 0.416 \text{ SL/CL}$.

The $D(4)$ scores are for nest sample means:

manchu ($n = 7$): 1.200 ± 0.092 [1.058, 1.342]

fennica ($n = 6$): 1.621 ± 0.171 [1.427, 1.840].

Queens of *manchu* were not available to the author but the data given by Agosti (1989) and Dlussky (1964) for five type queens of *dluskyi* provide further arguments for a heterospecificity of *manchu* and *fennica*:

	Type queens	
	<i>fennica</i> (n = 3)	<i>dluskyi</i> (n = 5)
Thoracic length <i>sensu</i> Agosti	2673 ± 39	2370 ± 40
Scape index <i>sensu</i> Agosti	98.9 ± 0.6	102.3 ± 2.1
Head index <i>sensu</i> Agosti	82.0 ± 0.6	79.0 ± 1.7

These data, in particular thoracic length, differ to an extent that is unusual for intraspecific variability known within the subgenus.

Formica fennica n. sp. differs from *Formica bruni* Kutter, 1967 by the much longer and much more dilute frontal and tergite pubescence, by the longer head, and the larger nHTFL; sometimes the acute occipital corners may be diagnostic. The separation of the two species' workers is possible even at the level of individuals by a linear discriminant score D(4) calculated as $D(4) = 0.206 \sqrt{\text{PDF}} + 0.109 \sqrt{\text{PDG}} + 0.078 \text{nHTFL} + 0.133 \text{CL/CW}$.

The D(4) scores are for worker individuals:

bruni (n = 161): 2.059 ± 0.148 [1.73, 2.47]

fennica (n = 27): 3.012 ± 0.206 [2.49, 3.35]

and for nest sample means:

bruni (n = 57): 2.056 ± 0.108 [1.84, 2.33]

fennica (n = 6): 3.026 ± 0.149 [2.86, 3.22].

The differences between the workers of *fennica* and *bruni* are repeated in the queens (Table 8). An additional difference is the significantly larger body size of the *fennica* queens. The zoogeography of both species is fundamentally different. *Formica bruni* represents a submediterranean-suboceanic type with European origin while *fennica* represents a north temperate-continental type with Siberian origin.

Single workers of extremely pilosity-reduced *exsecta* morphs may be confused with *fennica*. However, nest sample means of three workers provide a save separation with the characters nCOXA (*exsecta* 2.6-15.5, *fennica* 0.4-1.4), TERG (*exsecta* 1.0-2.33, *fennica* 3.0-4.0), OseSet

(*exsecta* 0.33-1.0, *fennica* 0-0.33), and ClySet (*exsecta* 2.0-4.5, *fennica* 1.0-2.0) as confirmed for 88 nest samples of *exsecta* and six nest samples of *fennica*. The usually more acute occipital corners of *fennica* are no reliable discriminator from *exsecta* because of big intraspecific variability of head shape in *Coptoformica*.

BIOLOGY AND DISTRIBUTION

Geographic range

F. fennica is apparently a continental, north temperate-montane faunal element. The type localities in Finland and Caucasus probably represent the western border of distribution. Agosti (1989) determined a Finnish sample from Alkkia (near Karvia), 62.11°N, 22.45°E, leg. Agosti 1986.08.05, as *Formica bruni*. The different zoogeography of *bruni* and the fact that Agosti did not distinguish *bruni* and *fennica* (he determined the Caucasian type colony of *fennica* as *bruni*) suggest that this sample represents the fourth known Finnish site of *fennica*.

Biology

A polycalic colony comprising 40 nests was found near Puhos/Finland on 13 July 1996. It spread over a fresh-dry grassland that was situated between the southern margin of a medium-aged *Betula* wood and the S-exposed slope of a road ditch. Plant species growing near the nests were *Dianthus* sp., *Prunella* sp., *Galium* sp., *Melampyrum nemorosum*, *Dactylis glomerata*, *Potentilla erecta*, *Scabiosa* sp., *Alchemilla* sp. The nest construction was of typical *Coptoformica* type and the largest nest mound measured 70 × 45 cm (diameter by height). Queens were deep in the soil and only three dealate queens could be collected at ground level. The Caucasian sample of *fennica* was found on a short-grassy, 20°N-exposed mountain pasture at 1600 m and collected from an isolated monodomous colony. The large size of the workers in this nest strongly suggests monogyny.

Formica bruni Kutter, 1967

TYPE LOCALITY. — Zermatt, Switzerland.

TYPE MATERIAL. — Syntypes 1 male, 4 queens, 3 workers (MZ) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 201 specimens (161 workers, 17 queens, 23 males) came from Sweden 25, Germany 8, France 23, Switzerland 105, Austria 28, Yugoslavia 9, Spain 3. Total number of specimens seen > 350.

DESCRIPTION

Worker (Figs 2-4; 15)

Medium-sized species (CL 1305 ± 72 , 1090-1484; CW 1244 ± 77 , 1033-1449). Head of average *Coptoformica* shape (CL/CW 1.050 ± 0.016 , 0.999-1.096). Scape rather long (SL/CL 1.013 ± 0.025 , 0.941-1.082). Setae only present on anterior clypeus, long decumbent pubescence hairs on frontolateral clypeus always present (ClySet 1.77 ± 0.49 , 1-3; ClyPub 3.79 ± 1.17 , 1.0-6.5; Figs 3; 15). Lateral semierect setae in the ocellar triangle rarely present (OceSet 22%). Eye hairs more or less developed, maximum eye hair length at least in few specimens of a nest sample > 10 μm (EyeHL 15.4 ± 5.2 , 4-29). Pubescence hairs in the ocellar triangle short and very dense (Fig. 4, sqrtPDF 4.40 ± 0.41 , 3.31-5.87). Craniad profile of forecoxae without or very few semierect setae (nCOXA 0.22 ± 0.55 , 0-3). Dorsal mesosoma, lateral metapleuron and ventrolateral propodeum without standing setae (nMET 0.00 ± 0.04 , 0-0.5). Outer edge of the hind tibial flexor side on the distal half with few subdecumbent setae (Fig. 2, nHTFL 4.11 ± 1.33 , 1.0-8.0). Semierect setae on gaster tergites usually beginning at posterior border of third or fourth tergite (TERG 3.23 ± 0.70 , 2-5). Pubescence density on first gaster tergite variable but usually rather low (sqrtPDG 6.36 ± 0.51 , 5.10-7.75).

Queen

Medium-sized (CL 1429 ± 37 , 1354-1488; CW 1430 ± 44 , 1340-1518; ML 2359 ± 91 , 2232-2535). Head slightly elongated, but shorter-headed specimens occur (CL/CW 1.000 ± 0.025 , 0.935-1.030), scape long (SL/CL 0.949 ± 0.016 , 0.926-0.982). Setae restricted to anterior clypeus. Clypeus lateral of the tentorial pit level with pubescence hairs surpassing the anterior margin by more than 10 μm . Lateral semierect setae in the ocellar triangle usually absent but

differentiation from pubescence difficult. Eye hairs relatively long (EyeHL 23.9 ± 4.8 , 16-34). Pubescence in the ocellar triangle short and extremely dense (sqrtPDF 3.46 ± 0.29 , 3.05-3.98). Occipital corners of head with subdecumbent to decumbent pubescence (OccHD 23.6 ± 5.4 , 12-30). Dorsal head surface relatively matt or weakly shining (GLANZ 1.33 ± 0.28 , 1.0-2.0). Craniad profile of forecoxae without or very few decumbent setae but differentiation from pubescence difficult (nCOXA 1.00 ± 1.02 , 0-3). Dorsum of head, mesosoma, and gaster with profuse and dense subdecumbent to decumbent pubescence. Dorsal mesosoma usually without clearly-defined strong setae but always with dense and long subdecumbent pubescence hairs single hairs of which approach in strength to setae (MnHL 73.2 ± 10.6 , 48-91). Outer edge of the hind tibial flexor side on the distal half with few subdecumbent setae and with short decumbent pubescence (nHTFL 3.41 ± 1.37 , 2.0-7.0). Semierect setae on gaster tergites usually beginning on the second to fourth tergite (TERG 2.88 ± 1.05 , 1-4). Pubescence on first gaster tergite very dense (sqrtPDG 4.54 ± 0.47 , 3.76-5.28).

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

Formica bruni shows rather constant characters throughout its geographic range and is usually well-separable from the other species. However, specimens with reduced eye hairs could be confused in particular with *foreli* and occasionally with *pressilabris*. In such cases, both species can be separated from *bruni* by the absence of projecting frontolateral clypeal pubescence and the absence of second level clypeal setae. *F. pressilabris* additionally differs by the shorter SL/CL and very sparse frontal pubescence. Details of the most useful characters to differentiate *bruni*, *foreli*, and *pressilabris* are given in Table 7. Queens of *bruni* are separable from each W Palaearctic species on the individual level; the data in Tables 7 and 8 need no further comment. The best difference to the long-headed, continental *manchu-fennica* group is the more dense frontal and

tergite pubescence and the significantly shorter head. The most reliable difference to large *foreli* queens with above-average EyeHL is the presence of lateral, projecting clypeal pubescence and of long and strong subdecumbent pubescence on promesonotum (MnHL > 40, in *foreli* always 0).

BIOLOGY AND DISTRIBUTION

Geographic range

Formica bruni represents a submediterranean-suboceanic type with European origin. The frequent confusion with *foreli* and *pressilabris* led to an underestimation of its distribution. 112 samples identified by the author came from altogether 50 localities in Spain, France, Italy, Yugoslavia, Switzerland, Austria, Germany and Sweden (two sites in Skåne). The French and Swiss Alps seem to be a distributional centre with 31 known sites. A record from the North Sea island of Terschelling/Netherlands (leg. Preuss) given by Agosti (1989) seems credible but needs confirmation. The vertical distribution in the W Alps ranges from 370 to 2150 m and is, as a consequence of grassland distribution, bimodal: 13 sites are situated at 708 ± 289 [370-1240] m and 18 sites at 1638 ± 231 [1380-2150] m.

Habitat selection

F. bruni is a specialised species of thermophilous, oligotrophic grasslands. In the W Alps, the main habitats of the colline/submontane population are xerothermous grasslands (preferentially on limestone) and the montane/subalpine population is usually found on sunny, S-exposed pastures or hay meadows. The German, Austrian, and Swedish populations were found in xerothermous to semidry grasslands on limestone or sand.

Status as threatened species

In Germany one (threatened by extinction). In Switzerland probably two (severely threatened). The causes of decline are similar as in *exsecta*.

Colony foundation

The host species for socially parasitic foundation is unknown. Isolated, monogynous colonies are rare, i.e. the transition from monogyny to poly-

gyny is apparently easier than in *exsecta*. As a rule, large polycalic colonies are found.

Nest construction

There is no difference to the normal *Coptoformica* type. The mounds do not reach the size known for *exsecta* and their diameter is normally < 50 cm. According to Feller (1985), nest entrances are always situated at the mound base. The subterranean part of an excavated summer nest showed a central vertical duct from which horizontal galleries branched off to chambers of 1-2 cm diameter that were distributed from near the surface down to 40 cm depth. Each chamber contained 2-3 queens.

Development and microclimatic requirements

In a polycalic colony near Martigny/Switzerland investigated by M. A. Schneider, oviposition usually begins in late March. Males and queens develop from the egg to the imago within 55-60 days (i.e., the first emerge from the pupae in late May). The developmental time of workers is 50 days in spring (first callows appear in mid-May) and 40 days in summer. The bulk of worker offspring ecloses from mid-July to mid-August.

Demography of nests and colonies

Two polycalic colonies in Switzerland comprised 250 nests/5644 m² (near Martigny, M.A. Schneider) and 61 nests/4000 m² (near Genolier, C. Feller). All nests were mutually friendly and exchanged populations. Two nests of 30-40 cm diameter were censused by Schneider for their winter population in late March. One nest contained 47500 workers and 79 queens and the other 51279 workers and 326 queens. Nest splitting in spring leads to a higher number of less populous summer nests. The corrected estimate of Feller (1985) for an "average" summer nest of 20 cm diameter was a total of 3500 workers and 24 queens (site near Genolier). Population concentration in autumn is believed to reduce winter mortality and dispersing in spring improves economic resource utilization and territory defence. 25% of the nests in Martigny and 20% of those in Genolier produced alates. A

bimodal but largely overlapping size distribution of the workers was observed by C. Feller; the larger workers preferentially performed Innendienst tasks and the smaller workers mainly Aussen-dienst tasks.

Swarming

In Central Europe, mature alates are found in the nests 19 July \pm 12.0 d (15 June-13 Aug, $n = 15$). Observations on swarming and mating were made in Switzerland (Schneider pers. comm.): in polycalic colonies only about 5% of females fly, the others are inseminated at the nest mounds. Micraners fly higher and farther than macraners. Macraners stay near the nest and transmit more sperm per mating: 220000 sperm cells against 120000 in micraners. Sufficient air temperatures given, swarming takes place from 7.00 to 11.00 h a.m., as soon as the first direct sunlight hits the mound surface. Completely clouded sky prevents the flight and beginning sunshine in the second half of the day can not release it.

Food sources

F. bruni can use a wide range of food sources. Trophobiosis with Aphidina is most important. Coccidae are used less frequent and also Cicadina sucking at the roots and lowest sprout parts of herbs are tended; in the latter case the Cicadina colonies are protected by walls of plant material. Floral and extrafloral nectaries of diverse plant species in the field layer are intensively exploited. Zoophagous activity may be considerable: different developmental stages of insects, spiders, and earthworms are consumed. The foraging activity is mainly diurnal. Nocturnal activity is 25% of the diurnal activity in mid-summer; in spring and autumn it is lower (Schneider pers. comm.). Foraging completely stops at surface temperatures $> 40^{\circ}\text{C}$. Different polygynous societies that do not exchange workers or broods may share territories and even food sources.

Formica pressilabris Nylander, 1846

Formica pressilabris Nylander, 1846

TYPE LOCALITY. — Helsingfors, Finland.

TYPE MATERIAL. — Lectotype by present designation 1 worker; paralectotypes 3 ♂♂, 5 workers (FMNH) [investigated].

Formica exsecta var. *rufomaculata* Ruzsky, 1895

TYPE LOCALITY. — Simbirsk (Ulyanovsk), Wolga River. New synonym.

TYPE MATERIAL. — Syntypes 4 workers (MHN and NHM Wien) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 465 specimens (382 workers, 64 queens, 19 males came from Sweden 44, Finland 92, Denmark 21, Netherlands 3, Germany 2, Poland 75, Slovakia 18, France 12, Switzerland 161, Slovenia 4, Russia 14, Caucasus 11, S Tibet 5). Total number of specimens seen > 600 .

DESCRIPTION

Worker (Figs 2-4; 14)

Rather small (CL 1280 ± 73 , 1046-1430; CW 1221 ± 70 , 1000-1371). Head shape of average *Coptoformica* type (CL/CW 1.049 ± 0.020 , 0.987-1.157). Scape short (SL/CL 0.974 ± 0.022 , 0.914-1.031). Clypeal setae restricted to anterior margin (Fig. 3), a second level seta in only 3% of specimens present (ClySet 1.03 ± 0.17 , 1-2). Clypeus lateral of the tentorial pit level only very exceptionally with single pubescence hairs surpassing the anterior margin by more than $10 \mu\text{m}$ (ClyPub 0.02 ± 0.16 , 0-1.5). Lateral semierect setae in the ocellar triangle always absent (OceSet 0%). Eye hairs fully absent or few minute hairs present (EyeHL 4.6 ± 1.9 , 0-9). Pubescence hairs in the ocellar triangle sparse (Figs 4; 14; sqrtPDF 6.28 ± 0.57 , 4.56-7.88). Craniad profile of fore-coxae without setae (nCOXA 0.0 ± 0.0). Lateral metapleuron and ventrolateral propodeum without standing setae (nMET 0.0 ± 0.0). Outer edge of the hind tibial flexor side with few semierect first order setae, second order setae absent (Fig. 2, nHTFL 2.77 ± 1.20 , 0-6.5). Erect setae on gaster often beginning on posterior margin of third tergite (TERG 3.16 ± 0.48 , 2-4). Pubescence on first gaster tergite relatively sparse (sqrtPDG 6.68 ± 0.39 , 5.79-7.86).

Queen

Size small (CL 1280 ± 39 , 1189-1354; CW 1293 ± 33 , 1197-1369; ML 2032 ± 67 , 1843-2192). Head proportions without peculiarities

(CL/CW 0.990 ± 0.020 , 0.950-1.031), scape very short (SL/CL 0.849 ± 0.019 , 0.822-0.892). Clypeal setae restricted to anterior margin (ClySet 1.02 ± 0.12 , 1-2). Clypeus lateral of the tentorial pit level without pubescence hairs surpassing the anterior margin by more than 10 μ m. Erect setae in the ocellar triangle absent. Eye hairs fully absent or very minute (EyeHL 4.5 ± 1.8 , 0-8). Pubescence in the ocellar triangle very sparse (sqrtPDF 6.09 ± 0.75 , 4.49-7.85). Occipital corners of head with fully appressed pubescence (OccHD 0.0 ± 0.0). Dorsal head surface shining (GLANZ 2.56 ± 0.42 , 1.5-3.0). Craniad profile of forecoxae without setae (nCOXA 0.0 ± 0.0). Dorsal mesosoma without standing setae (MnHL 0.0 ± 0.0), only with appressed, dilute pubescence. Outer edge of the hind tibial flexor side with very few suberect to subdecumbent first order setae, second order setae absent (nHTFL 1.31 ± 0.698 , 0-3.5). Erect setae on gaster tergites beginning at the posterior margins of third to fifth tergite (TERG 3.77 ± 0.53 , 3-5). Pubescence on first gaster tergite sparse (sqrtPDG 7.37 ± 0.66 , 5.48-8.60). Whole body smooth and shining.

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

The four syntype workers of *Formica exsecta* var. *rufomaculata* Ruzsky, 1895, stored in MHN and NHM Wien, labelled "*F. pressilabris* Nyl. var. *rufomaculata* Ruzsky, *Ssimbirsk* (Ruzsky)" have the following sample means: CL 1338, SL/CL 0.944, CL/CW 1.056, EyeHL 5.3, TERG 3.0, nCOXA 0.0, nHTFL 1.8, nMET 0.0, sqrtPDF 6.10, sqrtPDG 6.43, ClySet 1.0, ClyPub 0.0, OceSet 0, i.e. *rufomaculata* is in splendid agreement with the character combination of *pressilabris* and well-separated from *foreli* in any diagnostic character. The syntypes have a completely reddish dorsum of head and a reddish base of first gaster tergite inducing Ruzsky to create a new taxon and misleading Dlussky (1964) to give it a species rank. Such a reduction of dark pigment is occasionally observed within several species of *Coptoformica* (e.g., *exsecta*, *foreli*, and *pressilabris*) and without taxonomic significance.

BIOLOGY AND DISTRIBUTION

Geographic range

Formica pressilabris represents a boreo-alpine-continental species. The boreal range goes north to 65°N in Fennoscandia and reaches with an atlantic extension Denmark and the Netherlands. The continental range (which is fully connected with the boreal range in S Finland and the E Baltic) goes west to central Poland and W Slovakia. There are no recent records from Germany and the species is most probably extinct. A sample with two workers and a male collected by M. Zwecker in the vicinity of Würzburg / N Bavaria in 1929 indicates that isolated relict populations may have survived outside the main ranges. The most eastern samples of *pressilabris* investigated come from Lake Baikal (105°E, 52°N) and S Tibet (exact locality not known; approximately 92°E, 28°N, elevation > 4000 m; German Tibet Expedition 1938/39; samples 13a-c and 14a-d). The alpine population is distributed in the Swiss, French, and Italian Alps at 1802 ± 200 m (1460-2250, n = 41; with 28 sites at 1750-2250 m).

Habitat selection

In all parts of its geographic range, within the boreo-continental or the alpine range, nests of *pressilabris* are found in semidry to fresh oligotrophic grassland. These are either pastures, alpine meadows, clearings within woodland, or continental steppes.

Status as threatened species

The population in the W Alps is obviously stable, though mechanical stress by intensive cattle pasturing and alpine sports can clearly reduce populations. The Dutch, Danish, Polish, and Slovakian populations are probably much more threatened but exact data are not available. Germany: Red List 0 (extinct), Switzerland: Red List 3 (threatened).

Colony foundation

There is very sparse direct evidence which *Serviformica* species is used for socially parasitic colony foundation; in the alpine range, *Formica*

lemanii is most certainly the major host. One nest sample from the Klausenpass / Switzerland (in coll. H. Kutter) still contained several *lemanii* workers. Monodomous nests seem to be more frequent in continental Russia and polygynous/ polycalic colonies are more abundant in Central Europe. Polycalic colonies may have very instable nest positions in habitats with resource limitation.

Nest construction

Mound construction is not fundamentally different from the normal *Coptoformica* type. Mound material may also include seeds, soil particles and tiny pebbles. The mounds are smaller than in *exsecta* and their diameter is normally < 40 cm. An exceptionally large polygynous nest observed in the Bieszczady Mountains (Czechowski 1975) had a diameter of 100 cm and must have contained several hundred queens. A nest excavated by Dlussky near Voronezh showed galleries mainly to a depth of 50 cm, but a vertical duct led to chambers in a depth of 110 cm which were probably used during hibernation or excessive summer drought. On Swiss mountain pastures with intensive cattle grazing and condensed soil, the epigaeic nest parts can be small and the subterranean parts are mainly excavated in the very solid root turf that gives some protection against mechanical damage. In the Bieszczady Mountains, nests were frequently found in deserted or poorly inhabited earth mounds of *Lasius flavus*.

Demography of nests and colonies

Polycalic colonies may comprise > 100 nests/ 2000 m² and two colonies mapped by Czechowski (1975) contained 74 nests/1250 m² and 60 nests/580 m². An exact census of nest populations has not been performed but the situation seems similar to *bruni* or *foreli*. According to Pamilo & Rosengren (1984), monodomous populations are monogynous, have a sex ratio of < = 1 : 1, and have mainly macraners. Polydomous populations are polygynous with related gynes, have a sex ratio > 1, and have mainly micraners. Diploid males were found in polydomous *pressilabris* colonies.

Swarming

With respect to the whole geographic range, alates are found in the nests July 31 ± 15.1 d (June 25–September 5, n = 16). In the Alps, the majority of alates occurs in the period July 17–August 5. In polycalic colonies of the Swiss Alps about 90% of females fly, the others are inseminated at the nest mounds (Schneider pers. comm.).

Schneider also discovered a mating place near Montana/Swiss Alps at 2100 m which was situated inside the territory of a polycalic colony. About 15 queens were waiting in tall grasses on the upper edge of a small grassy slope bordering a small grassy plateau. The males patrolled at the top level of grasses in the lee position of queens, apparently for a better perception of queen sex pheromones.

Intra- and interspecific behaviour

Polycalic colonies frequently exchange populations and show no aggressivity to members of distant polygynous nests of the same colony.

Food sources

The main energy supply is provided by trophobiosis with any suitable species of Aphidae while predatory activity is usually less important. Aphid colonies are guarded and adult beetles of *Coccinella septempunctata* are attacked by the ants. Large aphid colonies at lower sprouts of plants can be sheltered by thin walls of plant material.

Formica foreli Emery, 1909

Formica exsecta pressilabris var. *foreli* Emery, 1909

TYPE LOCALITY. — Vaux near Morges, Switzerland, leg. Forel.

TYPE MATERIAL. — Holotype worker (MCSN) [investigated].

Formica naefi Kutter, 1957. New synonym.

TYPE LOCALITY. — Scuol-Pradella (Bain Jonnair), Switzerland

TYPE MATERIAL. — Syntypes 13 males, 5 queens, > 80 workers (MZ) [investigated].

Formica tamarae Dlussky, 1964. New synonym.

TYPE LOCALITY. — Omaló, Caucasus, leg. Zhizhilashvili.

TYPE MATERIAL. — Paratype and topotypical samples leg. Zhizhilashvili & Seifert [investigated].

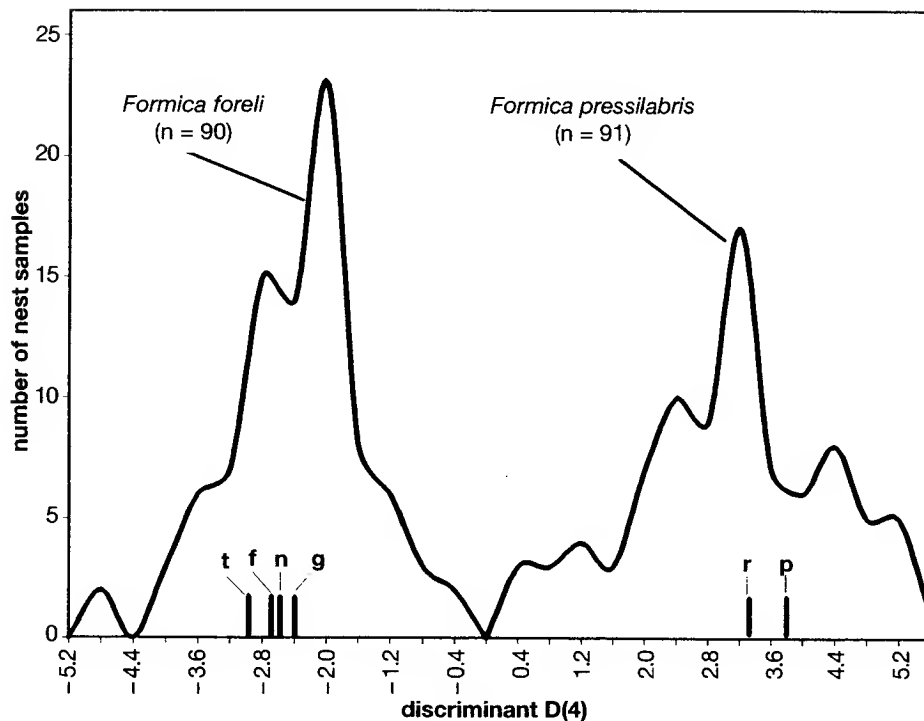


FIG. 6. — Discriminant score D(4) calculated with the characters sqrtPDF, sqrtPDG, SL/CS, and TERG to separate *Formica foreli* and *pressilabris* worker nest samples; the bars mark the position of the following type material: n, type series of *F. naefi* Kutter, 1957; g, type series of *F. goesswaldi* Kutter, 1967; f, holotype of *F. foreli* Emery, 1909; t, topotypical series of *F. tamarae* Dlussky, 1964; p, type series of *F. pressilabris* Nylander, 1846.

Formica goesswaldi Kutter, 1967. New synonym.

TYPE LOCALITY. — Soglio in Val Bregaglia, Switzerland.
TYPE MATERIAL. — Syntypes 20 males, 3 queens, 56 workers (MZ) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 421 specimens (330 workers, 69 queens, 22 males) came from Sweden 42, Germany 190, Czechia 8, Slovakia 7, Switzerland 124, Austria 4, Spain 8, Turkey 16, and Caucasus 22. Total number of specimens seen > 600.

DESCRIPTION

Worker (Figs 3; 4; 7; 9; 13; 16)

Rather small (CL 1288 ± 79 , 1013-1472; CW 1219 ± 77 , 981-1371). Head moderately elongated (CL/CW 1.057 ± 0.020 , 0.991-1.120). Scape rather long (SL/CL 1.008 ± 0.023 , 0.937-1.083). Clypeal setae restricted to anterior margin (Figs 3; 16), a small second level seta is in 7% of specimens present (ClySet 1.08 ± 0.27 , 1-2). Clypeus lateral of the tentorial pit level only very exceptionally with single pubescence hairs surpassing the anterior margin by more than 10 μ m

(ClyPub 0.04 ± 0.23 , 0-2.0, Fig. 16). Lateral semierect setae in the ocellar triangle always absent (OceSet 0%). Eye hairs fully absent or few minute hairs present (EyeHL 5.0 ± 2.1 , 0-11; Fig. 9). Pubescence hairs in the ocellar triangle dense (sqrtPDF 4.44 ± 0.44 , 3.36-6.16; Figs 4; 13). Craniad profile of forecoxae without setae (nCOXA 0.0 ± 0.0). Lateral metapleuron and ventrolateral propodeum without standing setae (nMET 0.0 ± 0.0). Outer edge of the hind tibial flexor side with few semierect first order setae, second order setae absent (nHTFL 2.67 ± 1.16 , 0-6.0). Erect setae on gaster often beginning on posterior margin of fourth tergite (TERG 3.88 ± 0.40 , 3-5). Pubescence on first gaster tergite variable, but usually relatively dense (sqrtPDG 6.09 ± 0.44 , 4.55-7.34).

Queen (Fig. 6)

Significantly larger than *pressilabris* (CL 1341 ± 38 , 1279-1464; CW 1362 ± 38 , 1286-

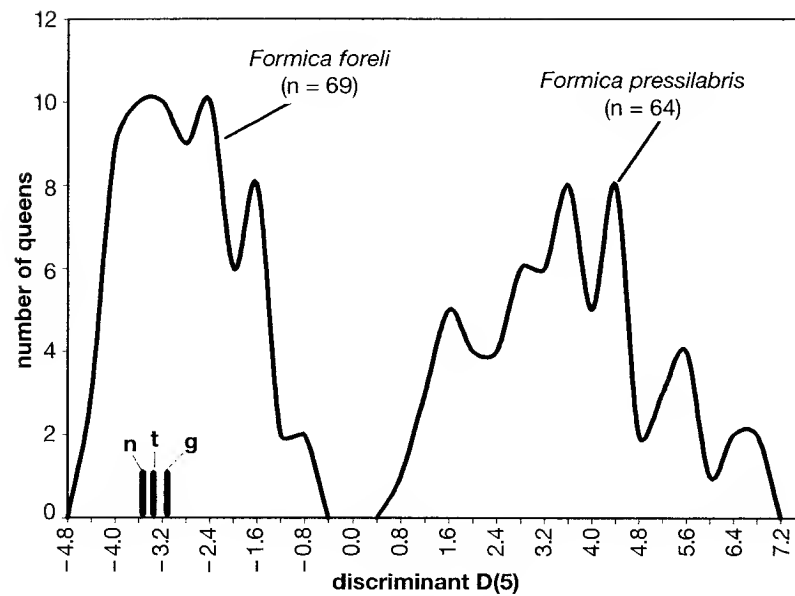


FIG. 7. — Discriminant score D(5) calculated with the characters sqrtPDF, sqrtPDG, SL/CL, ML, and GLANZ to separate *Formica foreli* and *pressilabris* queens. The bars mark the position of the following type material: **n**, type series of *F. naefi* Kutter; **g**, type series of *F. goesswaldi* Kutter; **t**, paratype of *F. tamarae* Dlussky.

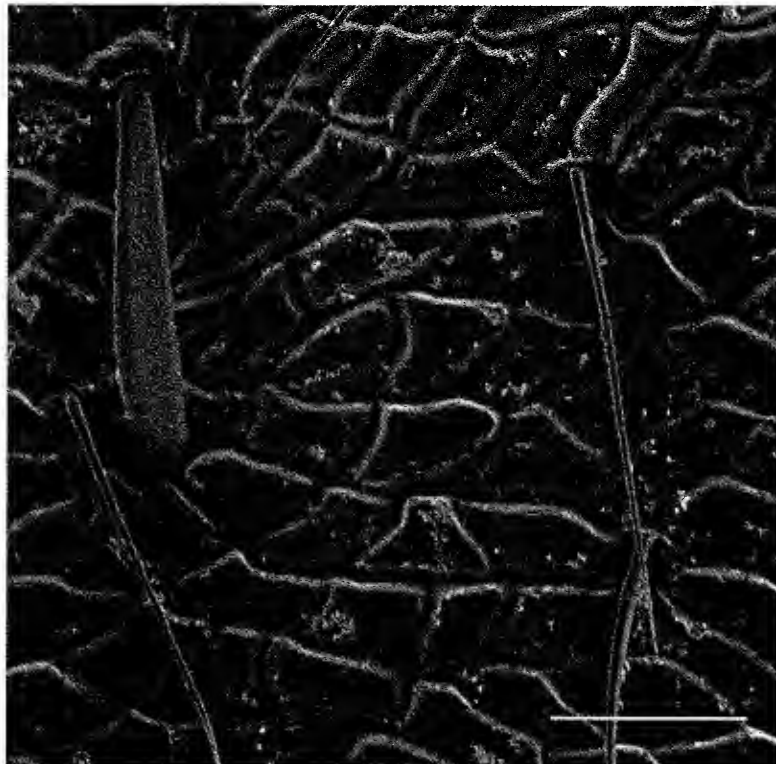


FIG. 8. — *Formica forsslundi* worker; SEM picture of a seta and three pubescence hairs in the ocellar region; the maximum strength of hairs is usually 1-2 μ m in pubescence and 4-8 μ m in setae. Scale bar: 20 μ m.

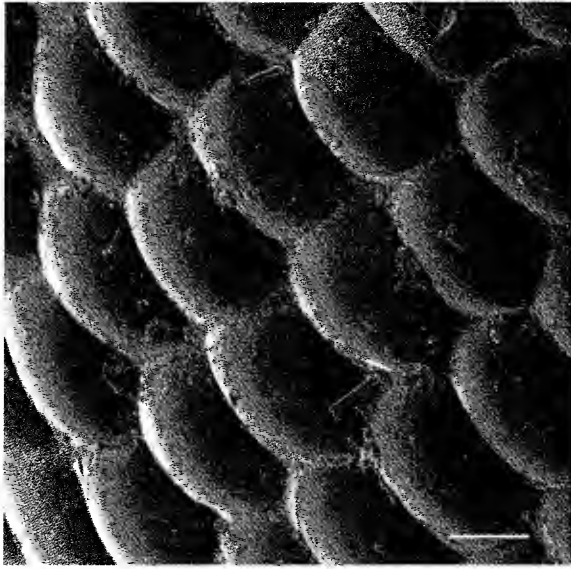


FIG. 9. — *Formica foreli* worker; SEM picture of short eye hairs; *F. foreli*, *pressilabris*, *forsslundi*, and *suecica* show frequently such hairs that are visible at stereo-microscopic magnifications higher than 150 x. Scale bar: 10 μ m.

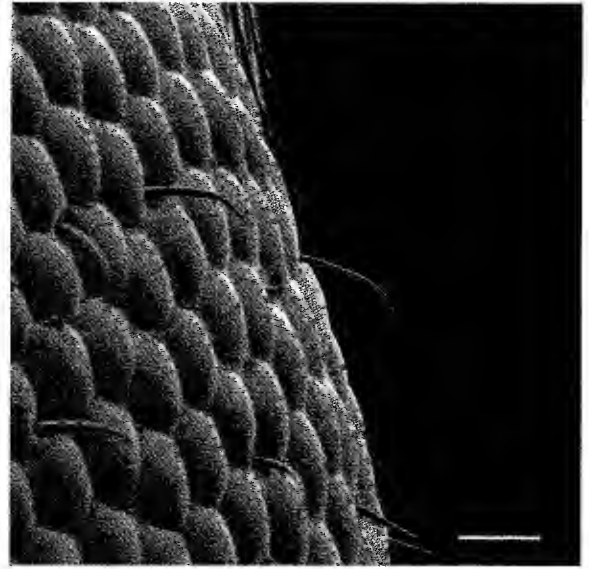


FIG. 10. — *Formica exsecta* worker; SEM picture of long and bent eye hairs. Scale bar: 20 μ m.

1479; ML 2227 ± 57 , 2107-2415). Head proportions of average *Coptoformica* type (CL/CW 0.985 ± 0.022 , 0.934-1.042), scape longer than in *pressilabris* (SL/CL 0.910 ± 0.023 , 0.857-0.962). Clypeal setae restricted to anterior margin, second level setae only exceptionally present (ClySet 1.01 ± 0.12 , 1-2). Clypeus lateral of the tentorial pit level without pubescence hairs surpassing the anterior margin by more than 10 μ m (ClyPub 0.0 ± 0.0). Erect setae in the ocellar triangle absent. Eye hairs absent or short (EyeHL 6.1 ± 3.6 , 0-21). Pubescence in the ocellar triangle very dense (sqrtPDF 4.03 ± 0.32 , 3.36-4.77). Occipital corners of head with fully appressed pubescence (OccHD 0.0 ± 0.0). Dorsal head surface variable, on average less shining than in *pressilabris* (GLANZ 1.87 ± 0.35 , 1.0-2.5). Craniad profile of forecoxae without setae (nCOXA 0.0 ± 0.0). Dorsal mesosonotum and scutellum without standing setae and only appressed pubescence (MnHL 0.0 ± 0.0). Outer edge of the hind tibial flexor side with very few suberect to subdecumbent first order setae, second order setae absent (nHTFL 1.23 ± 0.62 0-2.5). Erect setae on gaster tergites usually begin-

ning at the posterior margins of fourth to fifth tergite (TERG 4.65 ± 0.56 , 2-5). Pubescence on first gaster tergite usually dense (sqrtPDG 5.42 ± 0.54 , 4.54-6.68). Whole body less shining than in *pressilabris*.

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

The holotype specimen of *Formica foreli* was collected by Forel at Vaux near Morges/Switzerland and is still present in MCSN Genova. Bondroit (1918) stated that queens of *foreli* are different from those of *pressilabris* by the dull body surface, the slightly larger size, and the more dense gaster pubescence, i.e. his differential diagnosis is in agreement with the species conception presented below as it is in agreement with the investigation of Emery's type worker. Agosti (1989) synonymised *Formica foreli* with *pressilabris*. One reason for his decision were three puzzling nest samples collected by Malicky near Montana/Switzerland which are stored in MZ. These samples represent mixed nests of *pressilabris* and *bruni*, which contain a large fraction of true hybrids *bruni* x *pressilabris*. A detailed argumenta-

TABLE 2. — Worker nest sample means of *Formica pressilabris* and *foreli*. Given are arithmetic mean \pm standard deviation [lower extreme, upper extreme]; n, number of evaluated nest samples. D(4) is a discriminant score calculated with the characters sqrtPDG, sqrtPDF, SL/CS and TERG.

	Worker nest sample means			
	<i>foreli</i> (n = 90)		<i>pressilabris</i> (n = 91)	
D(4)	- 2.784 \pm 0.951	[-5.27, -0.55]	3.444 \pm 1.384	[0.26, 6.80]
sqrtPDH	4.432 \pm 0.316	[3.72, 5.16]	6.315 \pm 0.386	[5.25, 7.18]
sqrtPDG	6.084 \pm 0.323	[4.98, 6.75]	6.676 \pm 0.279	[6.01, 7.31]
SL/CS	1.0354 \pm 0.0172	[0.991, 1.081]	0.9954 \pm 0.0192	[0.952, 1.036]
TERG	3.882 \pm 0.259	[3.00, 4.33]	3.119 \pm 0.359	[2.00, 4.00]
CL	1283 \pm 70	[1114, 1452]	1280 \pm 50	[1157, 1384]
CL/CW	1.0568 \pm 0.0153	[1.020, 1.092]	1.0476 \pm 0.0149	[1.000, 1.078]

TABLE 3. — Data of queen individuals of *Formica pressilabris* and *foreli* from the W Palaearctic. Given are arithmetic mean \pm standard deviation [lower extreme, upper extreme]; n, number of evaluated specimens. D(5) is a canonical discriminant score calculated with the characters sqrtPDG, sqrtPDF, SL/CL, ML, and GLANZ.

	Individual queens			
	<i>foreli</i> (n = 69)		<i>pressilabris</i> (n = 64)	
D(5)	- 2.821 \pm 0.923	[-4.32, -0.68]	3.587 \pm 1.486	[0.74, 6.80]
sqrtPDH	4.04 \pm 0.30	[3.42, 4.76]	6.059 \pm 0.719	[4.49, 7.81]
sqrtPDG	5.45 \pm 0.57	[4.54, 6.68]	7.366 \pm 0.664	[5.48, 8.60]
SL/CL	0.908 \pm 0.022	[0.858, 0.947]	0.849 \pm 0.018	[0.822, 0.892]
ML	2223 \pm 55	[2107, 2345]	2031 \pm 66	[1843, 2197]
GLANZ	1.82 \pm 0.36	[1.0, 2.5]	2.56 \pm 0.42	[1.5, 3.0]

tion leading to this conclusion was presented elsewhere (Seifert 1999). The second reason for Agosti's synonymisation were Swedish *foreli* and *pressilabris* samples with ambiguous gaster pubescence. Such samples are not rare in S Sweden but, based upon character combinations, they can be allocated to either *foreli* or *pressilabris* in a similar way as in other geographic regions (see below). Significant differences in external morphology, zoogeography, and habitat selection give convincing evidence for a heterospecificity of *foreli* and *pressilabris*. The worker of *foreli* differs by a much more dense frontal pubescence, a significantly denser tergite pubescence, the more caudal position of tergite setae, and a longer scape. In these diagnostic characters, the holotype specimen of *foreli* fits very well to the population average with SL/CL 1.025, Terg 4.0, sqrtPDF 4.59 and sqrtPDG 6.07. A discriminant score D(4) calculated with the characters sqrtPDF, sqrtPDG, TERG, and SL/CS provides a clear separation of both species in 181 investigated W Palaearctic nest sam-

ples (Table 2; Fig. 6). The D(4) of the type series of *goesswaldi* and *naefi*, of the holotype of *foreli*, and of the topotypical series of *tamarae* are fully within the cluster defined here for *Formica foreli* while the type series of *pressilabris* and *rufomaculata* are clearly within the *pressilabris* cluster (Fig. 6). Queens of *foreli* and *pressilabris* are separable on the individual level by the characters sqrtPDF, sqrtPDG, SL/CL, ML, and GLANZ. A discriminant score D(5) calculated with these characters provides a clear distinction (Table 3). All available type queens of *goesswaldi* and *naefi*, and one paratype queen of *tamarae* have D(5) values very distant from the *pressilabris* cluster (Fig. 7). Further evidence for a heterospecificity of *foreli* and *pressilabris* is provided by zoogeography and habitat selection. *Formica pressilabris* represents a boreo-alpine-continental and *foreli* a submediterranean species with northern range expansion. Zones of geographic overlap are rather small and known from S Sweden, W Slovakia, and the W Alps. The external morphology of *foreli* and

TABLE 4. — Comparison of the workers of different geographic populations of *Formica foreli* which have been described as bona species. Given are arithmetic mean \pm standard deviation [lower extreme, upper extreme]; n, number of evaluated specimens.

	Unterengadin (Switzerland) <i>naefi</i> (n = 57)	ValBregaglia (Switzerland) <i>goesswaldi</i> (n = 23)	Omaló Caucasus <i>tamarae</i> (n = 21)	all regions <i>foreli</i> (n = 330)
CL	1308 \pm 90 [1134, 1472]	1269 \pm 49 [1148, 1364]	1334 \pm 83 [1098, 1458]	1288 \pm 79 [1013, 1472]
SL/CL	1.014 \pm 0.018 [0.975, 1.056]	0.999 \pm 0.018 [0.965, 1.039]	1.001 \pm 0.021 [0.955, 1.030]	1.007 \pm 0.023 [0.937, 1.083]
CL/CW	1.042 \pm 0.017 [1.009, 1.080]	1.072 \pm 0.015 [1.046, 1.107]	1.060 \pm 0.019 [1.018, 1.120]	1.057 \pm 0.020 [0.991, 1.120]
EyeHL	5.6 \pm 1.9 [0, 11]	5.2 \pm 2.0 [0, 8]	5.4 \pm 1.3 [4, 10]	5.0 \pm 2.1 [0, 11]
TERG	3.75 \pm 0.43 [3, 4]	4.00 \pm 0.00 [4, 4]	3.57 \pm 0.60 [3, 5]	3.88 \pm 0.40 [3, 5]
nCOXA	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]
nHTFL	3.22 \pm 1.11 [1.0, 6.0]	2.04 \pm 0.956 [0.5, 5.0]	2.45 \pm 0.96 [1.0, 4.5]	2.67 \pm 1.16 [0, 6.0]
nMET	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0 \pm 0 [0, 0]
sqrtPDF	4.21 \pm 0.28 [3.65, 4.85]	4.54 \pm 0.43 [3.84, 5.92]	4.47 \pm 0.39 [3.80, 5.10]	4.44 \pm 0.44 [3.36, 6.16]
sqrtPDG	5.98 \pm 0.44 [4.62, 6.77]	5.93 \pm 0.24 [5.50, 6.32]	6.26 \pm 0.45 [5.63, 7.34]	6.09 \pm 0.44 [4.55, 7.34]
ClySet	1.01 \pm 0.10 [1, 2]	1.00 \pm 0.00 [1, 1]	1.00 \pm 0.00 [1, 1]	1.08 \pm 0.27 [1, 2]
ClyPub	0.01 \pm 0.07 [0, 0.5]	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0.04 \pm 0.23 [0, 2.0]
OceSet	0%	0%	0%	0%

pressilabris samples from within and from outside the overlap zones does not differ significantly indicating that both species do not hybridise in detectable frequencies. The vertical distribution in the W Alps is very weakly overlapping. *F. foreli* usually occurs below 1600 m and is preferentially a species of warm valleys on spots with very xerothermous mediterranean floral elements. *F. pressilabris*, in contrast, mainly occurs in altitudes of 1750–2250 m and is a species of thermophilic mountain meadows and pastures with elements of boreo-alpine flora. Vaux near Morges, the type locality of *foreli*, is situated at 552 m. This fact gives additional evidence that *foreli* cannot be referred to *pressilabris*.

The synonymisation of *Formica goesswaldi*, *naefi*, and *tamarae* with *foreli* needs explanation. The investigated topotypical material of *goesswaldi* from Soglio and Vicosoprano/Val Bregaglia com-

prised five nest samples with 23 workers and three queens. The population of *Formica naefi* was studied in 14 nest samples with 57 workers and in 13 queens from the terra typica in the Unterengadin (Pradella/Scuol, Bain Jonnair/Scuol, Ramosch) and included all available types. *Formica tamarae* was studied in five nest samples with 21 workers and one paratype queen from the type locality Omaló/Caucasus. The data of Table 4 show only weak differences between the considered populations in the 13 evaluated characters which cannot even justify a subspecies rank. *Formica tamarae* is fully identical with the Central European *foreli* except for the slightly lower TERG data. The only difference of *goesswaldi* is the larger CL/CW that is, however, within the known range of variation in *foreli*. *Formica naefi* deviates by a significantly lower CL/CW and sqrtPDF but again these data do not exceed the range known in *foreli*.

TABLE 5. — Comparison of the queens of different geographic populations of *Formica foreli* which have been described as bona species. Given are arithmetic mean \pm standard deviation [lower extreme, upper extreme]; n, number of evaluated specimens.

	Unterengadin (Switzerland) <i>naefi</i> (n = 13)	Soglio (Switzerland) <i>goesswaldi</i> (n = 3)	Omaló (Caucasus) <i>tamarae</i> (n = 1)	all regions <i>foreli</i> (n = 69)
CL	1337 \pm 39 [1279, 1397]	1360 \pm 28 [1341, 1393]	1325	1341 \pm 38 [1279, 1464]
CW	1377 \pm 39 [1306, 1430]	1370 \pm 14 [1353, 1379]	1349	1362 \pm 38 [1286, 1479]
ML	2234 \pm 55 [2107, 2307]	2293 \pm 45 [2260, 2345]	2246	2227 \pm 57 [2107, 2415]
CL/CW	0.972 \pm 0.022 [0.934, 1.001]	0.993 \pm 0.020 [0.972, 1.012]	0.982	0.985 \pm 0.022 [0.934, 1.042]
SL/CL	0.922 \pm 0.020 [0.874, 0.947]	0.912 \pm 0.009 [0.902, 0.920]	0.944	0.910 \pm 0.023 [0.857, 0.962]
EyeHL	6.2 \pm 1.7 [5, 10]	6.7 \pm 1.2 [6, 8]	6	6.1 \pm 3.6 [0, 21]
GLANZ	1.84 \pm 0.24 [1.3-2.2]	1.57 \pm 0.40 [1.2-2.0]	1.5	1.87 \pm 0.35 [1.0, 2.5]
OccHD	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0	0.0 \pm 0.0 [0, 0]
MnHL	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0	0.0 \pm 0.0 [0, 0]
nCOXA	0.00 \pm 0.00 [0, 0]	0.00 \pm 0.00 [0, 0]	0	0.0 \pm 0.0 [0, 0]
TERG	4.62 \pm 0.51 [4, 5]	4.33 \pm 0.58 [4, 5]	4	4.65 \pm 0.56 [2, 5]
nHTFL	1.35 \pm 0.66 [0.5, 2.5]	1.00 \pm 0.50 [0.5-1.5]	1.5	1.23 \pm 0.62 [0, 2.5]
sqrtPDF	3.91 \pm 0.30 [3.48, 4.33]	3.96 \pm 0.09 [3.85, 4.03]	4.30	4.03 \pm 0.32 [3.36, 4.77]
sqrtPDG	5.12 \pm 0.36 [4.54, 5.89]	5.78 \pm 0.46 [5.26, 6.15]	5.96	5.42 \pm 0.54 [4.54, 6.68]

The situation in the queens is similar (Table 5). In none of the 12 characters evaluated is a difference suggesting a heterospecific identity of the four taxa. The elongation of the head in *goesswaldi* considered as diagnostic by Kutter (1977) is within the range known for *foreli* as it is the broadening of head in *naefi*. Differences in mesosoma shape, pigmentation, and scale shape, which were considered as diagnostic by Kutter, are in fact invalidated by the high intraspecific variation of these characters. In one character, however, the topotypical queens of *naefi* show an unusual deviation: they have a significantly larger eye size ($p < 0.001$). The ratio $(EL + EW)/(CL + CW)$ is 0.293 ± 0.007 [0.280-0.306] in 13 *naefi* queens from the Unterengadin and is 0.282 ± 0.007 [0.267-0.296] in 37 *foreli* queens from outside this region. The weak deviations of this relatively isolated popula-

tion in the Swiss Alps (which is actually threatened by extinction!) are interpreted here as consequence of bottle-necking events in the past and not as indication for a heterospecific status.

BIOLOGY AND DISTRIBUTION

Geographic range

Formica foreli represents a submediterranean species with northern range expansion during warmer climatic periods and subsequent splitting into isolated populations after regional extinction. It is known from N Spain, N Italy, Anatolia, the Caucasus, the W Alps, S Moravia, and W Slovakia. Reliable records from the German countries refer to an isolated population in Thüringen, two local populations in N Sachsen, larger populations in Brandenburg and the southern Mecklenburg-Vorpommern, and two

local populations in Schleswig-Holstein. An isolated northern population exists in NE Zealand/Denmark and Skåne/S Sweden with nine sites known. The population in the W Alps is restricted to valleys with xerothermous local climate in altitudes of 1181 ± 348 m (552-1780), ($n = 10$). In more southern latitudes (Anatolia) it goes up to 2200 m.

Habitat selection

F. foreli is a species of open oligotrophic and xerothermous grasslands mainly on sand, but also on limestone and other geological outcrop. The different zoogeography and much more expressed xerothermy of *foreli* compared to *pressilabris* is reflected by plant sociology. In all habitats studied at least some indicator plants for strong xerothermy such as *Festuca cinerea*, *Festuca ovina*, *Euphorbia cyparissias*, *Hieracium pilosella*, *Echium vulgare*, or *Eryngium campestre* were present. Very strong polycalic colonies in Brandenburg were observed to extend their nesting area into mesophilic grassland and light woodland but became extinct in the latter after full closure of the canopy.

Status as threatened species

Formica foreli is one of the most endangered species of the group. In Switzerland it is threatened by extinction. In Germany it has the same status, though the populations in Brandenburg and Mecklenburg-Vorpommern seem less endangered. The habitat destruction is mainly caused by intensive use of mineral fertilisers and liquid manure, high atmospheric nitrogen immission, decline of sheep pasturing and traditional cut-meadow management, intensifying of cattle pasturing, and afforestation programs.

Colony foundation

Four pins with *Formica foreli* workers from the type series of *Formica naefi* (labelled "Bain Jonnair, 10.7.54, Kutter-I") carry four workers of *Formica lemani* and one worker of *Formica lusatica*. The equal labelling should indicate a nest sample but the mode of sampling is not explicitly stated. Observations of Kutter (1957, 1969) in an laboratory arena with nests of *lemanii* and *fore-*

li (his *naefi*) showed an eudulotic behaviour of *foreli* with subsequent killing of the *lemanii* queen. It seems possible that eudulotic behaviour can also occur in nature (callows at least can be taken) and that mixed nests must not necessarily indicate a preceeding socially parasitic colony foundation by a single *foreli* queen. Habitat selection and zoogeography of *foreli* should exclude *lemanii* as primary host species except for few alpine populations. The main host species in the whole geographic range should be either *fusca*, *cunicularia*, or *rufibarbis*.

Nest construction

There is no difference from the normal *Coptoformica* type. The mounds do not reach the size known for *exsecta* and their diameter is usually < 50 cm. The diameter of the subterranean part of the largest nest was 80 cm. On very xerothermous spots of sand dunes or sandy moraines, where the field layer is very sparse, nests may entirely lack any vegetable cover and are only circumscribed by simple entrances in the soil surface. Nests in an intensive sheep pasture near Carwitz/Germany had constructed their subterranean galleries within the solidified root bale of vegetation to increase the resistance against trampling.

Demography of nests and colonies

No reliable information on the nest population is available but figures similar to *bruni* are expected. The tendency towards polygyny and polycaly is very expressed. The largest polycalic colonies in Brandenburg comprised 100 nests/2500 m² and 78 nests/1200 m². Polycalic colonies have a sex ratio > 1 and produce mainly micraners.

Swarming

Alates were observed in the nest 14.2 July \pm 24.9 d (12 June-24 Aug, $n = 10$) which is somewhat earlier than in *pressilabris*. Modalities and timing of swarming are unknown.

Intra- and interspecific behaviour

F. foreli is very aggressive and territorial against other territorial *Formica* species and *Lasius*.

Food sources

Workers of a large polycalic colony at the margin of a light forest in Brandenburg visited in large files Aphidae on *Pinus silvestris* and *Betula pendula* trees.

Formica pisarskii Dlussky, 1964

TYPE LOCALITY. — Songino (24 km SW of Ulan Bator), Mongolia.

TYPE MATERIAL. — Syntypes 1 queen, 10 workers (ZMLSU) (ZIPAS) (MZ No. 3297-3299) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated five nest samples with 17 workers and one queen originate from Songino, Somon Bajandelger, and Gorchii in Mongolia. Total number of specimens seen 25.

DESCRIPTION

Worker

Medium-sized (CL 1322 ± 54 , 1200-1384). Head elongated (CL/CW 1.069 ± 0.020 , 1.039-1.109). Rather long scape (SL/CL 1.009 ± 0.020 , 0.971-1.043). Whole clypeus from anterior to caudal parts with scattered setae (ClySet 4.47 ± 0.52 , 4-5). Clypeus lateral of the tentorial pit level without or very few pubescence hairs surpassing the anterior margin by $> 10 \mu\text{m}$. Lateral semierect setae in the ocellar triangle usually present (OceSet 93%). Eye hairs short or absent (EyeHL 7.2 ± 5.5 , 0-19). Pubescence in the ocellar triangle very dilute (sqrtPDF 7.11 ± 0.45 , 6.47-7.84). Craniad profile of forecoxae with few semierect setae (nCOXA 3.74 ± 1.08 , 2-6). Dorsal pronotum always with few standing setae (nPN 7.23 ± 3.30 , 4-16). Dorsal crest of petiole with few setae. Lateral metapleuron and ventrolateral propodeum only occasionally with single setae (nMET 0.03 ± 0.12 , 0-0.5). Outer edge of the hind tibial flexor side conspicuously hairy (nHTFL 8.06 ± 0.93 , 7.0-10.5). Semierect setae on gaster tergites always beginning on the first tergite (TERG 1.0 ± 0.0) and distributed over its whole surface. Pubescence distance on first gaster tergite very large (sqrtPDG 7.76 ± 0.43 , 7.04-8.84).

Queen

(One paratype queen). Very small (CL 1270, CW 1221, ML 2099). Head long (CL/CW 1.040), scape rather long (SL/CL 0.898). Clypeus from anterior to posterior portions with scattered standing setae (ClySet 4). Clypeus lateral of the tentorial pit level without pubescence hairs surpassing the anterior margin by $> 10 \mu\text{m}$. Lateral semierect setae in the ocellar triangle present. Eye hairs very short and sparse (EyeHL 7). Pubescence in the ocellar triangle extremely dilute (sqrtPDF 7.84). Occipital corners of head with appressed pubescence (OccHD 0.0). Dorsal head brilliantly shining (GLANZ 3.0); whole body very dark and shining, almost without microsculpture. Craniad profile of forecoxae with few setae (nCOXA 2.0). Promesonotum with many standing setae (nPN 14, MnHL 99). Outer edge of the hind tibial flexor side conspicuously hairy (nHTFL 9.0). Semi-erect setae on gaster tergites beginning on the first tergite (TERG 1.00) and not restricted to its caudal margin. Pubescence distance on first gaster tergite extremely large (sqrtPDG 8.11).

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

F. pisarskii is a species with a unique character combination. There is no other species in the genus with workers combining strongly developed clypeal and pronotal setae with reduced eye hairs and extremely large frontal and gastral pubescence distance. The queens can only be confused with those of *suecica* and *forsslundi* but *pisarskii* differs from the first by the extremely large PDF and PDG and the elongated head and from the latter by the presence of posterior clypeal setae and the large SL/CW (0.934, in *forsslundi* 0.770-0.888).

BIOLOGY AND DISTRIBUTION

The known distribution is limited to Mongolia. Dlussky (1965) mentioned two records from in Central Siberia (Chitinskaya oblast') and East Siberia (Yakutsk) of which I did not see voucher specimens. As habitats are reported by Pisarski

and Dlussky southern slopes of hill tops with sparse grassy vegetation. The nests were constructed either as small mounds of normal *Coptoformica* type (Dlussky) or below stones without epigeic structures (Pisarski).

Formica forsslundi Lohmander, 1949

Formica forsslundi Lohmander, 1949

TYPE LOCALITY. — Närke, Värmland, Västergötland, Sweden.

TYPE MATERIAL. — No types available in the museums of Göteborg and Stockholm [identification by original description].

Formica forsslundi strawinskii Petal, 1962. Synonym.

TYPE LOCALITY. — Rakowskie Bagno near Frampol, district Lublin, SE Poland.

TYPE MATERIAL. — Paratypes worker and queen (ZIPAS) [investigated].

Formica brunneonitida Dlussky, 1964. New synonym.

TYPE LOCALITY. — Cherulen Buudal, Mongolia.

TYPE MATERIAL. — Syntypes (ZMLSU ZIPAS ; MZ) [investigated].

Formica fossilabris Dlussky, 1965

TYPE LOCALITY. — NE Tibet: southern coast of Lake Koko Nur [synonymy by original description of workers and by investigation of a worker sample from the locus typicus].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 125 specimens (94 workers, 18 queens, 13 males) came from Sweden 27, Finland 33, Denmark 3, Germany 9, Poland 11, Switzerland 16, Caucasus 16, Mongolia 7, and N Tibet 3. Total number of specimens seen > 200.

DESCRIPTION

Worker (Figs 2; 8; 11)

Rather small (CL 1281 ± 70 , 1024-1404). Head shape of average *Coptoformica* type (CL/CW 1.051 ± 0.018 , 1.007-1.099). Scape rather short (SL/CL 0.987 ± 0.019 , 0.944-1.035); in the Caucasian population extremely short (SL/CL 0.947 ± 0.023 , 0.912-0.979). Clypeus only in anterior area with standing setae, caudal setae always absent (ClySet 1.84 ± 0.52 , 1-3). Clypeus lateral of the tentorial pit level frequently with few pubescence hairs surpassing the anterior margin by more than > 10 μm ; in the Caucasian population such hairs are fully absent; ClyPub

1.31 ± 1.21 , 0-6.0. Lateral semierect setae in the ocellar triangle in many specimens absent (OceSet 47%). Eyes usually without or with few microscopically short hairs, in the Mongolian and Tibetan samples few longer hairs are frequently present; EyeHL 6.6 ± 3.2 , 0-25. Pubescence hairs in the ocellar triangle extremely sparse (sqrtPDF 6.96 ± 0.84 , 5.63-9.80; Fig. 11). Craniad profile of forecoxae usually with single semierect setae which are in the Caucasian population fully absent; nCOXA 1.31 ± 1.35 , 0-4.5. Lateral metapleuron and ventrolateral propodeum as a rule without standing setae (nMET 0.01 ± 0.05 , 0-0.5). Outer edge of the hind tibial flexor side with several semierect first order setae, second order setae absent (Fig. 2, nHTFL 5.82 ± 1.14 , 3.0-8.5). Erect setae on gaster tergites usually beginning on the first tergite (TERG 1.16 ± 0.40 , 1-3). Pubescence on first gaster tergite variable but usually very sparse (sqrtPDG 7.09 ± 0.55 , 5.62-8.24). Promesonotum frequently with a blackish patch with diffuse margin.

Queen

Size very small (CL 1223 ± 43 , 1160-1307; CW 1248 ± 28 , 1210-1299; ML 1885 ± 69 , 1784-2003). Head proportions without peculiarities (CL/CW 0.980 ± 0.029 , 0.911-1.022). Scape rather short (SL/CL 0.867 ± 0.019 , 0.831-0.897), in the two Caucasian queens extremely short (SL/CL 0.796, 0.797). Clypeal setae restricted to anterior portion, second level setae usually present. Erect setae in the ocellar triangle may be present. Eye hairs fully absent or very minute (EyeHL 6.2 ± 2.5 , 0-10). Pubescence in the ocellar triangle usually extremely sparse (sqrtPDF 5.95 ± 0.61 , 4.80-6.96). Occipital corners of head with decumbent to appressed pubescence (OccHD 6.0 ± 6.4 , 0-16). Dorsal head surface brilliantly shining (GLANZ 2.94 ± 0.16 , 2.5-3.0). Craniad profile of forecoxae with few semierect setae, differentiation between setae and large pubescence hairs often difficult, making setae counts problematic (nCOXA 2.06 ± 2.54 , 0-9.0). Dorsal mesosoma frequently with standing setae (MnHL

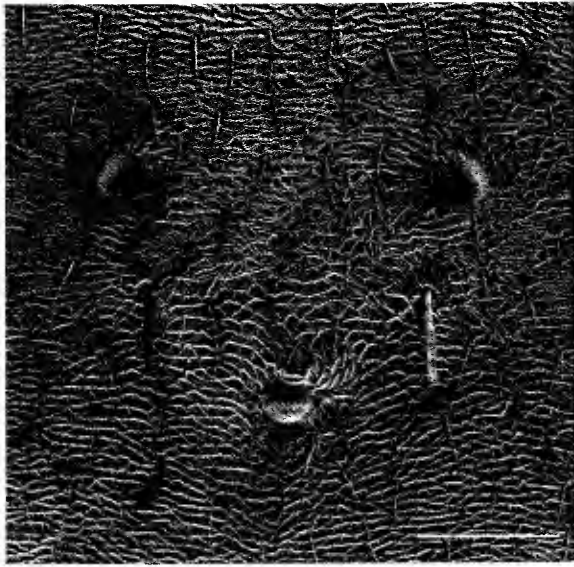


FIG. 11. — *Formica forsslundi* worker. SEM picture of the ocellar triangle showing a very sparse pubescence. The 2 setae seen in this specimen are frequently absent in *forsslundi*. Scale bar: 100 μ m.

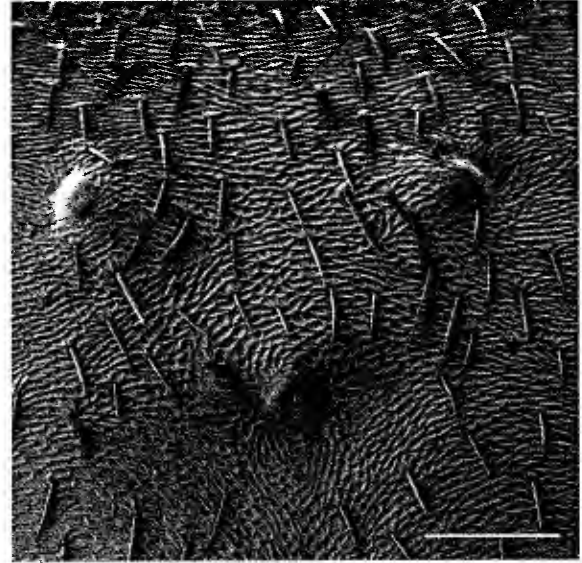


FIG. 12. — *Formica fennica* worker; SEM picture of the ocellar triangle showing a very long and sparse pubescence. Scale bar: 100 μ m.

85.9 \pm 54.1, 0-166). Outer edge of the hind tibial flexor side with several suberect to subdecumbent 1st order setae, second order setae absent (nHTFL 4.11 \pm 1.89, 2.0-8.5). Erect setae on gaster tergites usually beginning on the first tergite (TERG 1.17 \pm 0.38, 1-2). Pubescence on first gaster tergite sparse (sqrtPDG 6.73 \pm 0.76, 5.06-8.07). Whole body smooth and shining, dark brown to blackish. Dorsal excision of petiole often deeply u-shaped.

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

The unavailability of types means no taxonomic risk in the case of *forsslundi*. The description of Lohmander (1949) and its statements on the peculiar habitat selection and nesting should leave no doubt which species is meant.

Four worker paratypes and one queen paratype of *Formica forsslundi* ssp. *strawinskii* Petal, 1962 from the bog Rakowskie Bagno in SE Poland do not differ in 13 numeric characters from the population means of Palearctic *forsslundi*. They only differ by above-average data of nCoxa and ClySet which are, however, fully within the range

of variability known for *forsslundi*. Apart from the problem of describing a subspecies from a locality within the range of the nominal form, Petal (1962) presented no evidence of taxonomic significance for the proposed differential characters.

Twelve paratype workers of *brunneonitida* Dlussky, 1964, labelled "Mongolia, Cherulen Buudal, 120 km E Ulan Bator, 7.VI.1962, leg. Pisarski No. 3384" and two other worker samples from Mongolia and NE Tibet strongly suggest a synonymy of *brunneonitida* with *forsslundi*. Dlussky (1964, 1965, 1967) did not state any differential character to *forsslundi*. In fact, the investigations of this revision could not demonstrate a difference between 74 European workers of *forsslundi* (= nominal population) and the 10 available Mongolian and N Tibetan workers (= *brunneonitida*) in the characters CL, SL/CL, TERG, nCOXA, nHTFL, nMET, sqrtPDF, sqrtPDG, ClySet, ClyPub, and OceSet even for the weak significance level of 0.05 if tested in a *t* test. A weakly significant difference for $p < 0.05$ is indicated for the larger CL/CW and EyeHL in the Central Asian population but the latter difference is not confirmed by a nonparametric

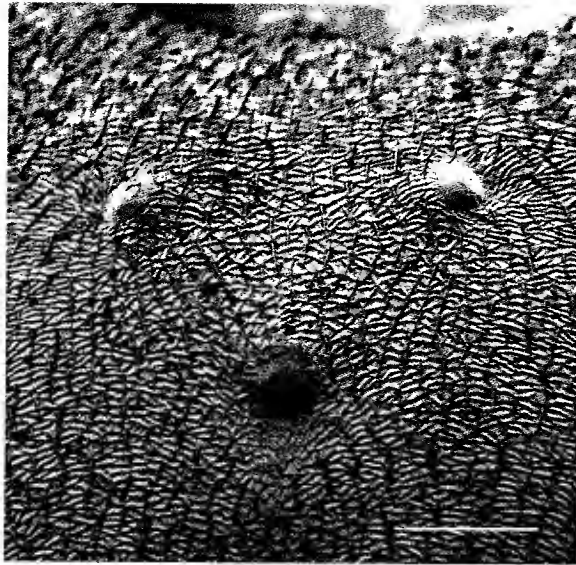


FIG. 13. — *Formica foreli* worker; SEM picture of the ocellar triangle showing a very dense and short pubescence. Scale bar: 100 μ m.

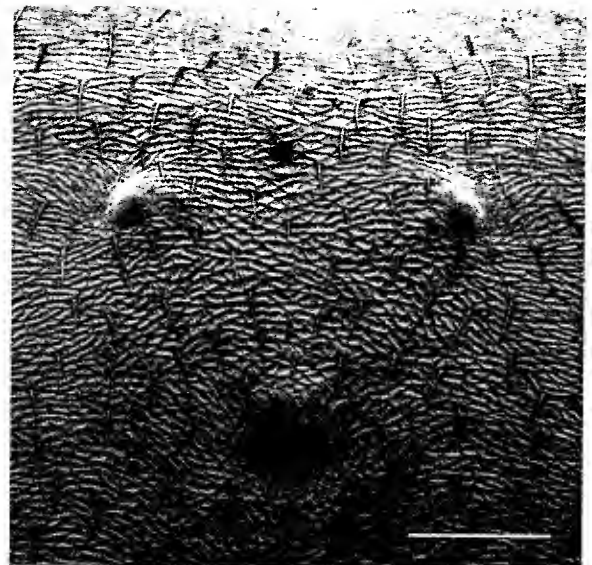


FIG. 14. — *Formica pressilabris* worker; SEM picture of the ocellar triangle showing a very sparse pubescence. Scale bar: 100 μ m.

U test. The following sequence of data compares the arithmetic mean \pm standard deviation for *brunneonitida* (before the comma) and *forsslundi* (after the comma): CL 1274 \pm 96, 1275 \pm 67; SL/CL 0.992 \pm 0.025, 0.987 \pm 0.018; CL/CW 1.061 \pm 0.015, 1.049 \pm 0.017; EyeHL 11.7 \pm 7.0, 6.1 \pm 1.7; TERG 1.30 \pm 0.48, 1.14 \pm 0.38; nCOXA 1.00 \pm 0.91, 1.53 \pm 1.38; nHTFL 6.45 \pm 1.14, 5.68 \pm 1.06; nMET 0 \pm 0, 0.02 \pm 0.13; sqrtPDF 7.24 \pm 0.84, 6.80 \pm 0.58; sqrtPDG 7.34 \pm 0.41, 7.01 \pm 0.57; ClySet 2.10 \pm 0.57, 1.88 \pm 0.48; ClyPub 1.05 \pm 1.23, 1.54 \pm 1.17; OceSet 50%, 52%. These data provide no argument to maintain even a subspecies status of *brunneonitida*. The alleged differences between *forsslundi* and *brunneonitida* in the number of maxillary palp segments (Agosti 1989) have no taxonomic significance because specimens with five and six maxillary palp segments do occur syntopically (and even intranidally) in W Palearctic *forsslundi*. Queens of *brunneonitida* were not available to the author but the structural and morphometric data given in the description of type material by Agosti are consistent with the characters of W Palearctic *forsslundi* queens. Agosti stated as only diagnostic difference of the

brunneonitida queen a “dorsally concavely excavated petiole which sides are never parallel”. Queens showing such petioles can be found in the European *forsslundi* population, e.g., in a sample from near Torskinge/Sweden. Furthermore there is much probability for the species *forsslundi* to occur much farther in the East because it shows cold hardiness, can nest in mineralic soil, and is bound to the host species *F. transcaucasica* that is widely distributed all over the subboreal and alpine Palearctic. The high similarities in habitat selection and zoogeography shown by *Formica forsslundi* and *uralensis* in the European range suggest that *forsslundi* could have a similarly wide Palearctic range as the latter species. The easily recognized *uralensis* is known to have a continuous range from subboreal W Europe to SE Siberia. The underrecording of *forsslundi* from Siberia seems to be more question of insufficient knowledge of determination characters or of the less eye-catching behaviour and nesting. The habit of preferentially nesting in temperate lowland Europe in peat bogs is, as in *uralensis*, a question of competitive displacement. Simple nests in mineralic soil without epigeic mound constructions, as they were reported by

Pisarski for the Mongolian type population of *brunneonitida*, are also observed occasionally in the W Palaearctic *forsslundi* population (Agosti 1989; Soerensen pers. comm.). As a consequence there is no morphological, biological, or zoogeographical argument for heterospecificity of *brunneonitida* from *forsslundi*.

Formica fossilabris Dlussky, 1965 has been described from a single worker sample collected by P. K. Kozlov at the southern coast of Lake Koko Nur/NE Tibet in August 1902. These types (said to be deposited in St Petersburg) were not available to the author. Instead a worker nest sample collected by A. Gebauer in the foot hills at the SW coast of Lake Koko Nur (37.00N, 99.53E, 3300 m) in June 1998 and the descriptions of type material by Dlussky (1965) and Agosti (1989) are used to infer a synonymy with *forsslundi*. According to these verbal descriptions and Dlussky's drawings, the setae characters on clypeus, head, mesosoma, and gaster, the morphometrics, and the eye pilosity are in agreement with the conception of *forsslundi* presented above. Dlussky stated as diagnostic character of *fossilabris* "the middle of anterior part of the clypeus with triangular impression with an "alley" of hairs, widening towards the apex". As already stated by Agosti and as stated above, clypeal shape is intraspecifically much too variable in *Coptoformica* to serve as diagnostic character and depressed triangular areas on anterior clypeus are no rare exceptions in W Palaearctic *forsslundi*. Dlussky's drawing of the holotype shows that the "alley of hairs widening towards the apex" is nothing but an usual arrangement of first, second and third level setae on anterior clypeus. Such arrangements are occasionally found in W Palaearctic *forsslundi* and seem to be less rare in the Asian population. A triangular impression in anterior clypeus is clearly developed in all three examined topotypical workers (leg. Gebauer) and the setae arrangement depicted by Dlussky is seen in one of these specimens. This sample fully matches the character combination of *forsslundi* and has the following means: CL 1348, CL/CW 1.054, SL/CL 0.974, EyeHL 7.0, TERG 1.0, nCOXA 2.2, nHTFL 7.0, nMET 0.0, sqrtPDF

7.77, sqrtPDG 7.38, ClySet 2.0, ClyPub 0.5, OceSet 67%. Hence it is most probable that *fossilabris* is a synonym of *forsslundi*.

The *forsslundi* population found on subalpine pastures of the Caucasus is most certainly fully isolated and shows an extremely short scape, no projecting pubescence hairs on lateral clypeus and reduced coxal pilosity. The extreme scape character in this population could be considered to justify erection of a new taxon. This is contradicted, however, by the high coincidence with the Palaearctic main population in the majority of characters and by the sharing of the same specific host species. The problem needs further investigation.

BIOLOGY AND DISTRIBUTION

Geographic range

A more or less coherent population is found in the subboreal European range, that spreads from N Germany (55°N) across Denmark to Fennoscandia north to 66°N. The Asian range is poorly known but there is no zoogeographic or biocenotic argument that the Siberian, Mongolian and Tibetan populations should not be connected with the W Palaearctic population across the continuous belt of subboreal biomes within the range of the abundant host species *F. transcaucasica*. A more southern range in the N Alps and SE Poland is documented by few, isolated bog populations between 47 and 51°N, which most certainly represent glacial relicts. In the Caucasus, an isolated subalpine population is found between 1500 and 2500 m. Such a subalpine population is also suspected to exist in the Alps between 1300 and 2200 m but the author could so far not see a voucher specimen.

Habitat selection

In the European range, *F. forsslundi* represents a rather stenopotent species and is bound to different types of open bogs, wet heathland, or mesophilic sand dunes. In Fennoscandia, nests are preferentially situated on organic soil in wetter central and peripheral parts of peat bogs with different species of *Ericaceae*. Towards the south, more marginal *Molinia* stands on mineralic soil

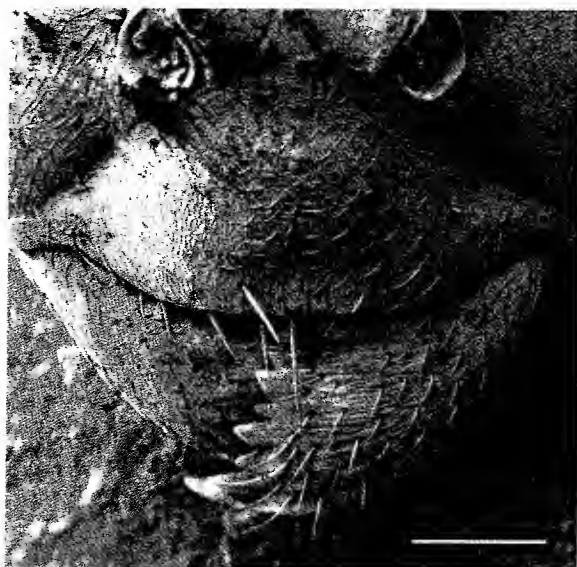


FIG. 15. — *Formica bruni* worker; SEM picture of clypeus showing first and second level seta and subdecumbent pubescence hairs surpassing anterolateral clypeal margin. Scale bar: 200 μ m.

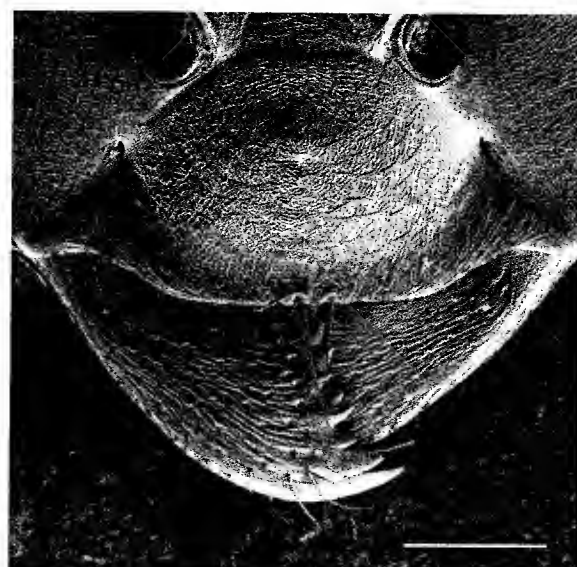


FIG. 16. — *Formica foreli* worker; SEM picture of clypeus with only first level seta and absence of subdecumbent pubescence hairs surpassing anterolateral clypeal margin. Scale bar: 200 μ m.

are preferred. In N Germany, a large population is found on semidry sand dunes with *Deschampsia*, *Molinia*, or *Empetrum*. The Caucasian population was found on subalpine to alpine pastures. In the cold steppes of Siberia, Mongolia and Tibet nest were found in xerothermous places on sandy soil with incomplete coverage of grasses but also in moister situations near to the ground water level.

Status as threatened species

In Germany and Switzerland threatened by extinction (Red List 1). Protection of bogs and cautious habitat management in heathland or mesophilic sand dunes is critical for the survival of this species.

Colony foundation

Formica transcaucasica seems to be the exclusive host species of *forsslundi* throughout its whole range in Fennoscandia, Germany, Switzerland, the Caucasus, and Tibet. Nests in the wettest parts of peat bogs seem to be preferentially monogynous. Polycalic colonies were observed in the Caucasus and Poland but seem to be generally rare.

Nest construction

In wetter parts of peat bogs, nests are usually found in bults with the virtual nest being restricted to a deep central cylinder that is typically roofed by a cover of *Ericaceae* leaves or white *Eriophorum* wool. The bult margin contains no nest galleries and is normally penetrated by *Ericaceae*, *Eriophorum*, and other grasses. Sometimes skewed "solar collectors" are constructed with plant material. Nests on mineralic soil are usually of the normal *Coptoformica* type made with finely-cut grass pieces. These nests have average dimensions of 20 \times 20 cm (height \times diameter) with the largest nests measuring 20 \times 40 cm. Sørensen (1993) noted rather instable nest positions in sand dune areas with an average of 25% abandoned nests per year. In a Swiss *Molinietum*, repeated mechanical stress by mowing has apparently caused a restriction of the nest galleries to subterranean parts (Agosti 1989). In Asia, simple soil nests without epigaeic mound constructions were observed in grasslands on sandy soil (Dlussky 1967) but the nest found by A. Gebauer in a moister site at Lake Koko Nur showed a typical mound construction with organic material.

Development and microclimatic requirements

Not studied. The nest spots in Europe indicate a higher tolerance against humidity compared to related species. The N German population started oviposition in mid April in the year 1998 (Soerensen pers. comm.).

Demography of nests and colonies

Only sparse information is available. Monogynous nests in bogs are not very populous: three nests excavated in Finland contained 500, 500, and 1500 workers. The largest population of *forsslundi* is known from the nature reserve Suederlueguemer Binnenduenen /N Germany with > 400 nests on 42 ha sand dune area and local densities of 84 nests/ha (Soerensen pers. comm.). No signs for polycaly (such as population exchange between the nests) were observed in this dense population.

Swarming

Not studied. Alates in the nests were found throughout the geographic range July 30.6 ± 9.9 d (July 15-August 25, n = 11).

Formica suecica Adlerz, 1902

TYPE LOCALITY. — Madelpad, Island of Alnön, near Sundsvall, Sweden.

MATERIAL EXAMINED. — 2 males, 1 queen, 6 workers (NHRM), 6 queens, 6 workers (MHN) [investigated].

GEOGRAPHIC ORIGIN OF THE MATERIAL STUDIED. — The numerically evaluated 92 specimens (62 workers, 28 queens, 3 males) came from Sweden 48, Finland 5, and Austria 30. Total number of specimens seen > 150.

DESCRIPTION

Worker (Figs 1E; 2)

Relatively large (CL 1345 ± 44, 1214-1427; CW 1327 ± 55, 1177-1463). Head significantly broader, and with distinctly more convex sides and more rounded occipital corners than in other *Coptoformica* species (Fig. 1E); CL/CW 1.015 ± 0.019, 0.951-1.066). Dorsum of head, in particular area between and near the frontal carinae, mildly shining. Scape rather long (SL/CL 1.033 ± 0.020, 0.981-1.075). Setae sparsely dis-

tributed over the whole clypeus (ClySet 4.0 ± 0.0, 4-4). Lateral semi-erect setae in the ocellar triangle frequently present (OceSet 72%). Eye hairs fully absent or few minute hairs present (EyeHL 6.2 ± 2.0, 0-13). Pubescence hairs in the ocellar triangle short and very dense (sqrtPDF 4.38 ± 0.21, 3.96-4.86). Craniad profile of forecoxae always with semierect setae (nCOXA 4.81 ± 1.47, 1-8). Single setae on lateral metapleuron and ventrolateral propodeum may be present (nMET 1.30 ± 0.88, 0-3.0). Outer edge of the hind tibial flexor side with suberect to subdecumbent first order setae, second order setae absent (Fig. 2, nHTFL 6.94 ± 1.02, 4.5-9.5). Erect setae on gaster tergites always beginning on the first tergite (TERG 1.0 ± 0.0, 1-1). Pubescence on first gaster tergite very dense (sqrtPDG 5.25 ± 0.38, 4.61-5.83). Dorsal head never with a contrasting reddish and blackish pigmentation pattern as usually seen in the other species; head colour normally homogeneous reddish, more rarely dark reddish brown.

Queen

Standing setae always well-separable from pubescence that is fully appressed on whole body. In most of the size data smaller than worker (CL 1252 ± 22, 1214-1285; CW 1280 ± 24, 1232-1318; ML 2061 ± 67, 1960-2175). Head not significantly broader than in other species (CL/CW 0.978 ± 0.010, 0.951-0.994), scape long (SL/CL 0.942 ± 0.014, 0.905-0.966). Setae sparsely distributed over the whole clypeus. Erect setae in the ocellar triangle usually present. Eye hairs absent or very minute (EyeHL 6.9 ± 2.6, 0-14). Pubescence in the ocellar triangle short and dense (sqrtPDF 3.98 ± 0.29, 3.58-5.03). Occipital corners of head with appressed pubescence (OccHD 0.6 ± 3.1, 0-16). Dorsal head surface shining (GLANZ 2.39 ± 0.35, 2.0-3.0). Craniad profile of forecoxae always with semi-erect setae (nCOXA 7.93 ± 1.32, 5.0-10.0). Dorsal mesosoma always with standing setae (MnHL 98.2 ± 10.3, 82-123). Outer edge of the hind tibial flexor side with suberect to subdecumbent first order setae, second order setae absent (nHTFL 6.15 ± 0.91, 4.5-8.0). Erect setae on

TABLE 6. — Morphometric data of worker individuals of species with mean EyeHL > 17 µm. Given are arithmetic mean ± standard deviation [lower extreme, upper extreme]; n, number of evaluated specimens.

	<i>exsecta</i> (n = 220)	<i>mesasiatica</i> (n = 18)	<i>fukaii</i> (n = 12)	<i>fennica</i> (n = 27)	<i>manchu</i> (n = 34)
CL	1419 ± 84 [1200, 1641]	1468 ± 61 [1359, 1582]	1481 ± 40 [1418, 1548]	1340 ± 110 [1087, 1514]	1375 ± 76 [1193, 1542]
SL/CL	1.008 ± 0.022 [0.931, 1.063]	1.027 ± 0.019 [0.989, 1.059]	1.046 ± 0.018 [1.018, 1.071]	0.989 ± 0.021 [0.945, 1.035]	1.013 ± 0.018 [0.966, 1.048]
CL/CW	1.042 ± 0.023 [0.979, 1.099]	1.038 ± 0.014 [1.002, 1.061]	1.048 ± 0.012 [1.025, 1.063]	1.067 ± 0.016 [1.036, 1.103]	1.073 ± 0.015 [1.044, 1.101]
EyeHL	27.0 ± 6.5 [0, 45]	35.7 ± 4.6 [30, 47]	28.5 ± 2.8 [25, 34]	23.2 ± 3.1 [17, 30]	27.9 ± 6.8 [12, 39]
TERG	1.19 ± 0.50 [1, 3]	1.00 ± 0.00 [1, 1]	2.75 ± 0.45 [2, 3]	3.37 ± 0.56 [3, 5]	2.91 ± 0.29 [2, 3]
nCOXA	8.86 ± 3.89 [0.5, 23]	4.58 ± 0.90 [3.0, 5.5]	0.08 ± 0.29 [0, 1]	0.91 ± 0.83 [0, 3]	1.30 ± 0.91 [0, 3.5]
nHTFL 1st ord.	10.97 ± 2.82 [5.0, 23]	9.50 ± 0.99 [8.0, 11.0]	7.20 ± 2.33 [1.0, 10]	8.13 ± 2.33 [4.0, 14]	4.78 ± 1.90 [1.0, 9.0]
nMET	1.86 ± 2.11 [0, 9]	3.61 ± 1.26 [1.5, 6.0]	0 ± 0	0 ± 0	0.04 ± 0.26 [0, 1.5]
sqrtPDF	5.69 ± 0.90 [3.78, 9.30]	3.99 ± 0.22 [3.58, 4.41]	4.02 ± 0.31 [3.65, 4.90]	6.68 ± 0.67 [5.19, 8.19]	5.95 ± 0.50 [4.95, 6.92]
sqrtPDG	6.82 ± 1.19 [3.93, 9.88]	4.43 ± 0.65 [3.72, 6.14]	3.93 ± 0.13 [3.68, 4.16]	7.89 ± 0.46 [6.99, 8.73]	7.57 ± 0.59 [6.46, 8.84]
ClySet	3.54 ± 1.08 [2, 5]	4.22 ± 0.43 [4, 5]	1.83 ± 0.39 [1, 2]	1.67 ± 0.56 [1, 3]	1.70 ± 0.64 [1, 3]
ClyPub	3.33 ± 1.10 [0.5, 5.5]	3.52 ± 0.84 [2.5, 5.0]	no data	2.09 ± 0.91 [1.0-6.5]	3.27 ± 1.82 [0.5, 7.0]
OceSet	92%	100%	33%	22%	12%

gaster tergites always beginning on the first tergite (TERG 1.0 ± 0.0, 1-1). Pubescence on first gaster tergite very dense (sqrtPDG 4.75 ± 0.41, 4.24-5.67). The dark brown body colour has often a yellowish tinge.

TAXONOMIC COMMENTS AND DIFFERENTIAL DIAGNOSIS

F. suecica is the most constant species of the subgenus (Tables 7; 9), showing a unique character combination. The disjunct Fennoscandian and Alpine populations show no differences (Glaser & Seifert 1999). The discrimination from *exsecta* is mainly given by the much smaller EyeHL and CL/CW, the absence of second order setae on hind tibia flexor profile (Fig. 2), the smaller sqrtPDF, the fully appressed pubescence on the occipital corners, and the more shining head surface. *F. exsecta* workers may sometimes approach *suecica* in a single character: either the

head length index may be reduced, the head colour can vary to homogeneous reddish, or eye hairs may be reduced. However, among > 1000 *exsecta* workers seen, not a single specimen showed a character combination inducing confusion with *suecica*.

BIOLOGY AND DISTRIBUTION

Geographic range

Formica suecica represents a boreo-alpine species. The known European distribution includes entire Fennoscandia between 56°N and 68°N, Estonia, and the region of Arkhangelsk. The only known Siberian site at Tevris (57.31°N, 72.20°E) seems disjunct but there is no argument that *suecica* is not continuously distributed from N Europe to Siberia within the zone of boreal coniferous forests. It is rarely collected and the insufficient knowledge of its character differences to *exsecta* could have led to under-

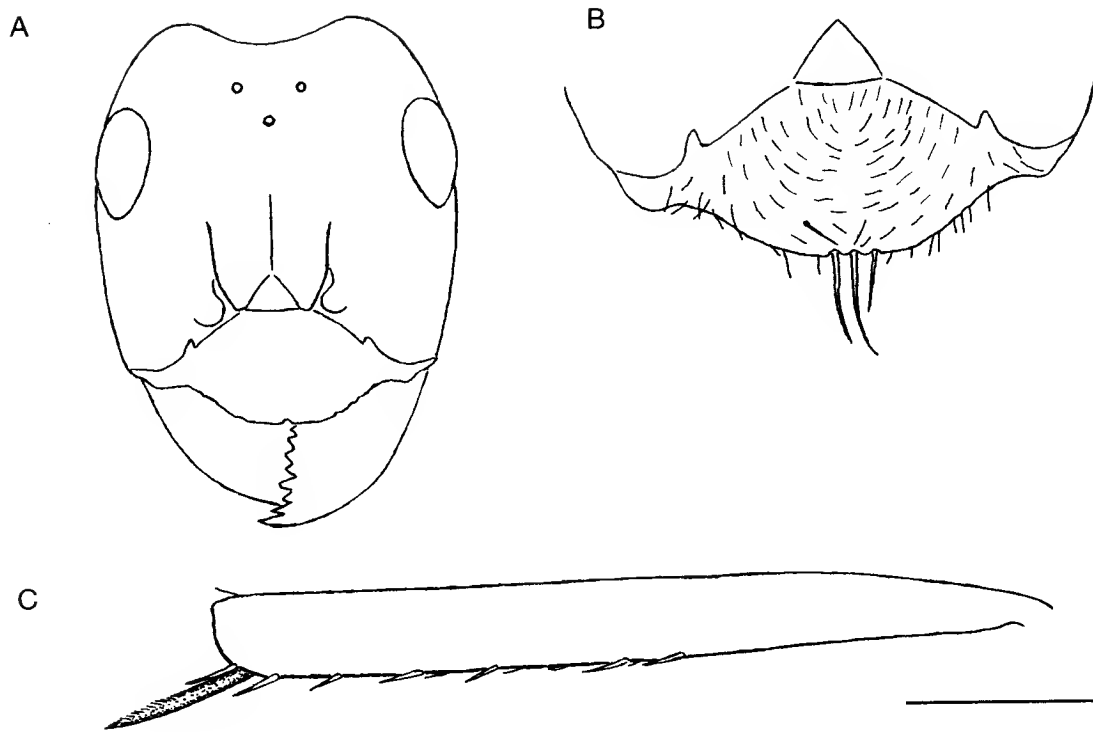


FIG. 17. — Syntype worker of *Formica manchui*; A, head; B, anterior clypeus; C, hind tibia, view not fully directed on the large tibial diameter, there is a slight tilt for better visualisation of setae on outer margin of flexor profile. Scale bar: A, 635 μ m; B, C, 400 μ m.

recording. *F. suecica* has been considered as exclusively boreal ant, but recently a disjunct Alpine population was discovered in the upper Ötztal/Austria at 1940–2200 m (Glaser & Seifert 1999).

Habitat selection

In Fennoscandia, *suecica* was frequently found at the sunny margins of bogs in the transition zone from turf to mineralic soil (42 nests), less frequently in sun-exposed heath-like habitat patches within woodland stands of *Picea abies*, *Abies alba*, or *Betula* on mineralic soil (23 nests), and exceptionally in a meadow (one nest) (data of Forsslund 1949 and Agosti 1989 combined with my own results). The only known alpine population at Obergurgel in the Ötztal/Tirol was found in habitats with very cold local climate. One habitat, a 19°N-exposed alpine heath with *Empetrum nigrum*, *Vaccinium myrtillus*, *Rhododendron ferrugineum*, *Juniperus*

sibiricus, and scattered old trees of *Pinus cembra*, has a mean annual air temperature of 2.1 °C with snow melting usually in late May. The other main habitat was N- or W-exposed alpine heath of *Vaccinium myrtillus*, *Rhododendron ferrugineum*, *Vaccinium vitis-idaea*, and grasses.

Status as threatened species

The population in the upper Ötztal is obviously very strong. *Suecica* is here the only *Coptoformica* species and codominant with *Formica lugubris* and *paralugubris*. In the Red List of Austrian ants it should have the status R (isolated population that is not directly endangered).

Colony foundation

Evidence as to which host species is used by the very small *suecica* queen for socially parasitic nest foundation is very scant. However, *Formica lemni* must be one of the hosts since it was the only

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Submitted on 3 July 1998;
accepted on 23 December 1999.